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dies on the Occipital Bone in Africa

THE OCCIPITAL CURVATURE IN FOSSIL MAN AND THE LIGHT
HROWS ON THE MORPHOGENESIS OF THE BUSHMAN

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evious studies in this series, exploring varying occipital curvature of over modern African crania, have demoned the existence of two phenotypically nct patterns in Negroes and Bushmen ias, '58a, '58b). The former group is acterized by marked flattening of the tal arc from lambda to opisthion, eas the Bush cranium has a strongly ed occiput. In young crania of both ps, however, there is very little difice of curvature and all skulls have gly bossed occiputs. Occipital flatten-n Negro crania sets in at about the of eruption of the first permanent , and continues until the *planoccipital* our of the adult is attained. Bush a, on the other hand, are not subject is flattening process and retain the ile *curvoccipital* contour into adult- (Tobias, '58c). The mechanism of ital flattening is shown to be a hinge-ment downwards along the lambdoid e, with compensatory endocranial cation and ectocranial resorption of djacent parts of the parietal bones ias, '59a).

is the purpose of the present paper to ire which of the two fundamental an occipital patterns is the older and, ice the phylogenetic trends in occipi-ariation. To this end, the occipital ture has been studied in 62 fossil and ossil hominid crania from Africa. For arison, data have been assembled on on-African fossil crania.

the second part of the paper, the mor-enesis of African cranial patterns is sed in the light of the evolutionary s revealed. In particular, light is n on the differing taxonomic valencies of occipital curvature and of other infantile or genetically retarded features of the Bush cranial morphology.

METHODS

Two curvature indices of the occipital bone have been derived from a single pair of measurements, the sagittal chord (S′3) and arc (S3) between lambda and opisthion.

The first index expresses the chord as a percentage of the arc [100(S′3/S3)].

The second index, Karl Pearson's Occipital Index (Oc.I.), expresses the percentage ratio of the radius of curvature of the occipital bone to the chord S′3. The assumption is made that the median sagittal curve from lambda to opisthion is an even curve, part of the circumference of a single circle. The Oc.I. is obtained from the formula;

$$\text{Oc.I.} = \frac{S3}{S'3}\sqrt{\frac{S3}{24(S3 - S'3)}}$$

or, given the size of S′3 and S3, it may be read off directly from tables compiled by Tildesley ('20–'21).

The history and usefulness of these indices are described and assessed elsewhere (Tobias, '58a, '59b).

MATERIALS

The materials available for the study of occipital indices in fossilized and protohistoric African crania are as follows:–

Australopithecus prometheus Dart. Specimen M.L.D.1 from Makapansgat (Boné and Dart, '55) kindly measured by Professor R. A. Dart.

Kanjera I. From Leakey ('35) and remeasured by the author.

Broken Hill (Rhodesian Man). From Morant ('28).

Singa. Measured by the author, with the permission of the Keeper of Geology, British Museum (Natural History).

Gamble's Cave IV. Measured by Leakey ('35).

Skildergat (Fish Hoek). Measured for the author by Dr. R. Singer. This cranium, formerly considered to belong to the Middle Stone Age, is now thought to belong to the Second Intermediate (Magosian-type) stage in the African cultural sequence agreed on by the 3rd Pan-African Congress on Prehistory at Livingstone (Clark, '57).

Naivasha. The human cranium from the Naivasha Railway Rock Shelter was measured by Leakey ('42) and re-measured by the author at the Coryndon Museum, Nairobi, in June, 1957, with the kind permission of Dr. Leakey. The cranium was originally attributed to the Upper Kenya Capsian "C" of the end-Palaeolithic, but it should perhaps be regarded as Upper Kenya Capsian "D" of the Kenya Mesolithic.

Asselar and *Mechta I.* Measured for the author by Dr. H. V. Vallois.

Afalou-bou-Rhummel. Occipital measurements were made by the author on 5 male and 4 female crania from Afalou, with the kind permission of the Director of the Institut de Paléontologie Humaine, Paris, Dr. H. V. Vallois.

Matjes River Wilton (South African Later Stone Age). From original measurements of two males and 4 females by Meiring ('37).

Mesolithic Elmenteitans, Neolithic East Africans and *Iron Age East Africans.* Indices were extracted mainly from data published by L. S. B. Leakey ('35, '45, '50). These 24 crania are made up of the following:

	Mesolithic	
Bromhead's Site, Elmenteita	4♂, 3♀	Leakey, '35
	Neolithic	
Makalia	1♂	Leakey, '35
Nakuru	1♂	Leakey, '35
Willey's Kopje	3♂	Leakey, '35
Hyrax Hill	1♂	Leakey, '45
Ngorongoro	3♂	Trevor (unpub.)
Njoro River	5♂, 2♀	Leakey and Leakey, '50
	Iron Age	
Hyrax Hill	1♂	Leakey, '45

Nyarindi (Kenya Smithfield). These crania, one male and one female, w measured by the author at the Coryn Museum, Nairobi, with the kind per sion of Dr. Leakey.

Cape Flats. Kindly measured by Dr Singer. This cranium from an old l surface below three feet of wind-bl sand is of indeterminate age (Drenn '29).

Tanganyika Proto-historic. Two n crania from Naberera and two male cra from Handeni were measured by the thor in the Anatomy Department, Make College, Kampala, Uganda, with the mission of Professor A. Galloway. Naberera crania do not include the nium described by Galloway ('33) un the place-name, Nebarara, but they w referred to by Fosbrooke ('57) and repo on by Galloway at the 3rd Pan-Afri Congress on Prehistory at Livingst (Clark, '57).

Kakamas Hottentots. Four males an females were especially measured by A. C. Hoffman, Director of the Natio Museum, Bloemfontein.

Istrice (Abyssinia). Measured by the thor at Nairobi in June, 1957. This published cranium was excavated by He de Monfreid in a cave between Harrar Diredawa, and handed over to the Cor don Museum by Dr. J. C. Trevor. The of the cranium is unknown.

RESULTS

Occipital curvature in fossil man

In table 1, the occipital indices of A can fossil and sub-fossil crania are giv and, for comparison, those of a num of non-African fossil crania. African fo range from *Australopithecus* to proto- toric and historic groups, whereas those non-African forms extend from *Pithec thropus* to Upper Palaeolithic Europ crania.

It is noteworthy that the majority fossil remains and *all* the *earlier* fo crania, both African and non-African, into the category of ultra-strong occip curvature with chord-arc indices be 80.5% (see categories proposed by Tob '58b). With these may be compared figures for *Australopithecus prometh* (Dart, '48). Professor R. A. Dart v

dly provided the author with the previously unpublished median sagittal chord l arc of the occipital bone (M.L.D.1) m Makapansgat, the bone being entire the median plane. The determination ambda in this specimen is rendered difilt by the presence of a series of lambd ossicles. However, the upper of two ssible points used by Dart coincides with point determined by the recommended hnique of Buxton and Morant ('33); mely, the point of intersection of three ncil lines following the general direction the sagittal and lambdoid sutures. This nt may be regarded as the closest apximation to lambda possible. From it occipital arc measures 85.0 mm and chord 68.0 mm, giving indices of .05 and 80.00. Thus, the occipital index *A. prometheus* falls well within the man range and, in fact, on the opposite le of the modern human range to that which fall most of the non-human priates measured by Morant (Pearson and vin, '24). On its occipital indices, *A. ometheus* falls with the more ancient pes of man from Africa.

The remains of Kanjera I, found in 1933 Leakey on the southern shore of the virondo Gulf of Lake Victoria, have a ong occipital bulge, indicated by the ord and arc measurements of 88 and 2 mm to the point of the break in the edian plane (Leakey, '35). These figes, though incomplete, yield indices of 6.11 and ?78.57. When I examined the iginal in the British Museum (Natural story) in 1955, I found that the reconuction of the deficient parts of the nual surface of the occipital fragment is ghly asymmetrical. Using the point of e break judged to be nearest to opisthion the median plane, I obtained measureents differing fractionally from Leakey's d yielding indices of 56.26 and 78.79.

The cranium of *Rhodesian Man* which is maged in the occipital area gives an proximate value of 54.5 for Oc.I. g. 1). This compares well with an dex of 55.0 in Macgregor's reconstrucn of Heidelberg Man from the Mauer andible and is the lowest value in the ble, save only for those of Naivasha and rice. In his original table of Pearson's .I., Morant gave a value of 68.0 for Rhodesian Man (Pearson and Davin, '24). This was, however, based on a cast and the correct value was quoted in his later papers (Morant, '27, '28).

Unfortunately, the occipital bones of other heavily-browed early South African fossils, *Florisbad* and *Saldanha*, are incomplete, as are the later crania from *Boskop* and from *Tuinplaats* (Springbok Flats).

The cranium from the railway rock shelter near *Naivasha* (Kenya) is partly synostosed in the lambda region. Leakey's ('42) estimate of the position of lambda yielded indices of 72.94 and 53.80, making this cranium the second most curvoccipital African skull on record. However, on examining the skull at the Coryndon Museum, Nairobi, in June, 1957, I determined a rather different position for lambda, which rendered indices of 74.64 and 54.30.

The *Singa* cranium was originally measured by Smith Woodward in 1938 and remeasured by Wells in 1951, but neither worker measured the occipital arc and chord. When in 1955, I was given facilities for working in Dr. K. P. Oakley's

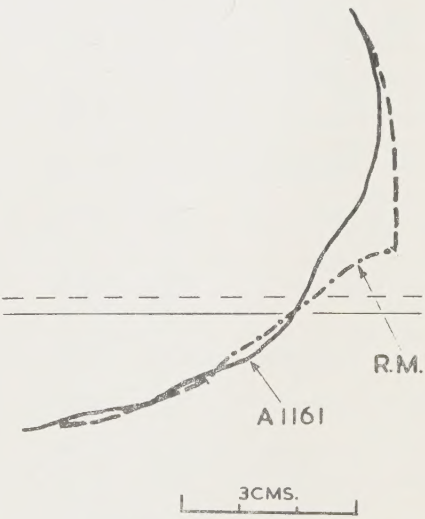


Fig. 1 Occipital contour of Rhodesian Man (R.M.) compared with that of a Bush-type cranium with similar occipital index. R. M., Rhodesian Man with occipital indices 75.17?? and 54.5??. A1161, Bush-type cranium with occipital indices 74.9 and 54.40. The portion of R.M. shown by a dot-and-dash line has been reconstructed. Note the contour of the occipital torus of R.M. in sharp contrast with the smooth surface of the Bush-type cranium.

TABLE 1

Occipital curvature of fossil crania from Africa and elsewhere

Cranium		100(S'3/S3)	Oc. I.	Reference
African zone				
Australopithecus prometheus		80.00	57.05	Dart, R. A. (pers. comm.)
Kanjera I		78.57	56.1	Leakey ('35)
		78.79	56.26	Tobias (unpub. remeasurement)
Florisbad		incomplete		—
Singa		77.22	55.38	Tobias (unpub.)
Broken Hill		75.17??	54.5??	Morant ('28)
Saldanha		incomplete		Singer (pers. comm.)
Springbok Flats		incomplete		—
Gamble's Cave IV		77.73	55.67	Leakey ('35)
Boskop		incomplete		—
Skildergat (Fish Hoek)		78.26	55.93	Singer (pers. comm.)
Naivasha		72.94??	53.80??	Leakey ('42)
		74.64??	54.30??	Tobias (unpub. remeasurment)
Mechta I	(♂)	80.80	57.64	Vallois (pers. comm., measured on cast)
Afalou-bou Rhummel	(5♂)	82.6	59.5	Tobias (unpub.)
	(4♀)	86.3	64.2	Tobias (unpub.)
Asselar		85.32	62.45	Vallois (pers. comm.)
Cape Flats		79.65	56.79	Singer (pers. comm.)
Plettenberg Bay		incomplete		Singer (pers. comm.)
Matjes River Wilton	(2♂)	82.0	59.0	Meiring ('37)
	(4♀)	84.1	62.0	Meiring ('37)
Nyarindi (Kenya	(1♂)	81.9	58.6	Tobias (unpub.)
Smithfield)	(1♀)	83.9	60.6	Tobias (unpub.)
Bromhead's Site				
(Mesolithic	(4♂)	81.3	58.4	Leakey ('35)
Elmenteitans)	(3♀)	83.9	60.7	Leakey ('35)
Willey's Kopje (Kenya Neolithic)	(3♂)	80.98	58.48	Leakey ('35)
Ngorongoro				
(Tanganyika	(3♂)	81.00	58.08	Trevor (pers. comm.)
"Neolithic")	(2♀)	86.25??	64.09??	Trevor (pers. comm.)
Njoro River Cave				
(Late stone age	(5♂)	77.75	55.74	Leakey ('50)
survival)	(2♀)	79.73	56.92	Leakey ('50)
Makalia II (Kenya Neolithic)	(♂)	80.17	57.19	Leakey ('35)
Nakuru IX (Kenya Neolithic)	(♂)	80.93	57.74	Leakey ('35)
Hyrax Hill				
(Kenya Neolithic)	(1♂)	83.90	60.63	Leakey and Leakey ('45)
(Kenya Iron Age)	(1♂)	82.22	58.89	Leakey and Leakey ('45)
Istrice (Abyssinia)		74.2	54.2	Tobias (unpub.)
Tanganyika (proto-historic—4)		85.78	63.47	Tobias (unpub.)
Kakamas Hottentots (? historic)	(4⚥)	82.6	59.6	Tobias, (based on measurements by A. C. Hoffman, pers. comm.)
Predynastic Egyptians				
(Naqada A and Q)	(84♂)	—	60.2	Pearson and Davin ('24)
(Naqada, B, T, and R)	(23♂)	—	60.5	

TABLE 1 (*Continued*)

Occipital curvature of fossil crania from Africa and elsewhere

Cranium		100(S'3/S3)	Oc. I.	Reference
Non-African zone				
ıecanthropus robustus		72.3	53.63	Weidenreich ('51)
ıecanthropus pekinensis III		77.78	55.67	Weidenreich ('43)
ıecanthropus pekinensis XI		73.50	53.96	Weidenreich ('43)
ıecanthropus pekinensis XII		72.88	53.78	Weidenreich ('43)
ıecanthropus pekinensis Iean (3)		74.72	54.47	Weidenreich ('43)
ınscombe		80.34	57.29	Measured on cast (Tobias)
ɔ I		72.3	53.64	Weidenreich ('51)
ɔ V		71.8	53.53	Weidenreich ('51)
ɔ VI		74.6	54.28	Weidenreich ('51)
ɔ IX		73.8	54.01	Weidenreich ('51)
ɔ X		?67.3	?53.05	Weidenreich ('51)
ɔ XI		72.4	53.69	Weidenreich ('51)
ɔ Mean (6)		72.0	53.70	Weidenreich ('51)
ingsdorf			?54.2	Morant ('27) from Weidenreich's measurements
raltar I		?76.51	?55.0	Morant ('27)
		76.89	55.21	McCown and Keith ('39)
Chapelle		78.42	56.0	Morant ('27)
		78.42	56.04	McCown and Keith ('39)
ıpina (child)			57.3	Morant ('27) from Gorjanovic-Kramberger's measurements
ɔūn I		?83.33	?60.00	McCown and Keith ('39)
ıūl I		82.86	59.56	McCown and Keith ('39)
ıūl IV		?70.49	?53.31	McCown and Keith ('39)
ıūl V		79.03	56.42	McCown and Keith ('39)
ıūl IX		?73.64	?53.99	McCown and Keith ('39)
ɔūn-Skhūl Mean (5)		77.87	56.66	
nbe-Capelle	(♂)	80.00	57.1	Morant ('30)
ɔtte des Enfants, Grimaldi	(♂)	?79.76	?56.9	Morant ('30)
Adolescent	(♂)	?81.45	??58.2	Morant ('30)
rma Grande II	(♂)	??83.12	??59.1	Morant ('30)
-Magnon I	(♂)	79.29	56.6	Morant ('30)
		79.37	56.62	McCown and Keith ('39)
utré I	(♀)	?78.35	?56.0	Morant ('30)
utré II	(♂)	??83.73	??60.5	Morant ('30)
utré III	(♂)	82.12	58.8	Morant ('30)
utré IV	(♂)	79.15	56.5	Morant ('30)
utré V	(♀)	76.23	54.9	Morant ('30)
dmost III	(♂)	?78.66	?56.2	Morant ('30)
dmost IV	(?♀)	81.46	58.2	Morant ('30)
dmost IX	(♂)	76.61	55.1	Morant ('30)
dmost X	(♀)	79.02	56.4	Morant ('30)
ıtsch I	(♂)	79.69	56.8	Morant ('30)
per Palaeolithic (Europe)				
Iean	(13♂)	80.79	57.9	Morant ('30)
Iean	(6♀)	80.61	58.0	Morant ('30)

laboratory in the British Museum (Natural History), I was able to re-measure the cranium, including the chord and arc dimensions. The values obtained were: occipital arc 135.0 mm and occipital chord 104.25 mm. These give indices of 77.22 and 55.38.

Earliest Indications of Occipital Flattening in Africa

The earliest *North African* crania to show some degree of occipital flattening are Late Palaeolithic (Upper Capsian or Ibero-Maurusian) crania from *Mechta-el-Arbi* and *Afalou-bou-Rhummel*, and the *Asselar* skull which is possibly Final Palaeolithic or early Neolithic (Boule and Vallois, '32). This Asselar skull which Boule and Vallois held to show "Boskopoid" features falls low in the list, its indices of 62.4 and 85.3 indicating only gentle curvature of the occiput. In this respect, then, it differs from the other representatives of the "Boskopoid" strain, Bushmen, Hottentots and, to a degree, Griquas, all of whom have low indices and pronounced curvature. In its modest occipital curve, the Asselar cranium shows an early approach to the cranial contour of the negroid peoples of West Africa.

Of *East African* remains, it is to the Kenya Smithfield crania of *Nyarindi* and to the Mesolithic Elmenteitans of *Bromhead's Site*, as well as to the Neolithic remains of *Willey's Kopje, Makalia, Nakuru, Hyrax Hill* and *Ngorongoro*, that we must turn in order to find the earliest traces of some occipital flattening.

In *Southern Africa*, the earliest example of occipital flattening is evident in the Wilton (Later Stone Age) crania described by Meiring from *Matjes River* ('37). This group stands out in marked contrast to the more curvoccipital Old Yellow South Africans who have retained their low occipital indices down to the present day.

The available evidence suggests, therefore, that highly-curved occipitals characterized African peoples almost to the end of the Palaeolithic (on the European system of nomenclature) and to the Later Stone Age (in the African terminology); in the Mesolithic and the Later Stone Age, the first crania showing a moderate degree of flattening appear.

Earliest occipital flattening in non-African crania

An examination of the non-African f sil data reveals that the earliest crania show some degree of flattening are Lev loiso-Mousterian and Upper Palaeolit (Aurignacian and Solutrean), but the te ency remains moderate through the M dalenian. Nevertheless, the mean valu for Upper Palaeolithic crania of Euro (♂ 80.79; ♀ 80.61) remain in the catego of strong, and only just outside the cl of ultra-strong occipital curvature.

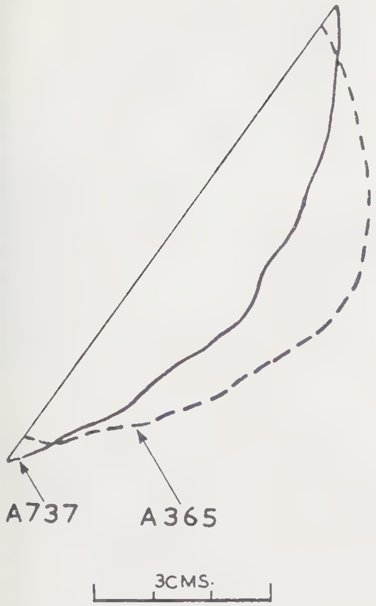
In Europe, too, the fossil evidence wou suggest that no flattening tendency of t occipital manifested itself until late in t Upper Palaeolithic.

Morant concludes from his survey European palaeolithic crania: "Not o of the values (of Oc.I.) given above extreme for a human skull, but there is clear suggestion that the archaic specime are characterized by unusually low indic —i.e., unusually protruding occipital bon —while the types which stand nearest them in this respect are the Upper Pala lithic and modern ones of Western E rope."

DISCUSSION

The evidence compiled from Africa this paper confirms the view of Mora ('30) that more ancient skulls possess we curved occipital bones. We might mod his statement that modern Western Eu peans stand nearest to the ancient cra in occipital curvature, by pointing out th crania of Old Yellow South Africans, pecially Bushmen, stand even closer them (fig. 2). In fact, *of all adequate studied racial series of crania anywhere the world, none surpasses those of t Bushmen in the degree to which th have preserved the extreme occipital cu vature of fossil man.*

It seems then that a strong occipi curvature is a very ancient human speci ization, serving to differentiate the hum line from that of the planoccipital anthr poid apes. This fact assumes considerab importance when we consider the crani classification which Frasetto ('09–'18), f lowing Sergi, based on patterns of front parietal and occipital growth. He point out that, in its development, each crani



ig. 2 The contour of a strongly curvoc-tal Bush skull (A365) with indices 76.23)(S'3/S3)] and 54.92 (Oc.I). For comparison, contour is superimposed on that of an ex-tionally planoccipital Zulu cranium (A737) h indices 93.1 and 83.97.

ılt-bone tends to pass through a phase extreme angulation or strong, pointed sing (the "fetal" stage), followed by a nding off to a more dome-like pro-erance ("juvenile" stage), finally to be laced by the smooth, arched contour the "adult" stage. These several shapes the individual vault-bones gave charac- to the calvaria as a whole, especially en seen from above. So, guided es-cially by the degree of bossing of the *rietal* bone, Frasetto recognized three ges of development of the whole vault, *pentagonoid* skull of the fetus or in-ıt, the *ovoid* contour of the juvenile and *ellipsoid* form of the adult, all in the lichocranial series. The corresponding ges in brachycranial skulls were *eury-ntagonoid, sphenoid* and *spheroid*. Not ery individual, however, attained the al ellipsoid or spheroid contour. Fe-les, for instance, retained more highly-ssed crania than males, even in adult-od. Mediterranean people frequently re-ned a pentagonoid vault throughout life, ereas this was much less common among Alpines and Nordics. In other words, individuals and races differed in the degree to which, in their ontogenies, they "outgrew" the fetal or infantile pattern. With the aid of a diagnostic set of 12 skulls presented by Frasetto to Professor R. A. Dart, Gear ('29) applied the Frasetto classification to South African crania. He showed that crania of Bantu-speaking Negroid peoples are most commonly ovoid, while those of Bushmen are generally pentagonoid. Frasetto's classification has been further usefully applied in South Africa at the hands of Dart ('37) and Eriksen ('57). The Frasetto-types could thus be used as purely static descriptive terms; but it was obvious that they might provide a clue to the pattern of growth and differentiation, so that the morphology would be capable of a more dynamic interpretation.

One such interpretation was soon to emerge, when Bolk ('29) suggested that fetalization (human neoteny or pedomorphism) had played a significant role in human evolution. The retention of fetal characters for long periods, and even into adulthood, was, he thought, one of the hallmarks distinguishing man from the apes. He went further and pointed out that, even among different human races of today, the degree of retention of infantile characters varied widely: a race with many retained infantile morphological traits was designated a "pedomorphic" race. One which has departed in many respects from the infantile pattern might be called "adultiform" or "gerontomorphic." Bolk stressed that Caucasoids and Mongoloids had many pedomorphic features, whereas Negroids had not.

Drennan ('29b) quickly pointed out that the South African Bush people and their antecedents show many pedomorphic features. Over subsequent years, various workers elaborated Drennan's theme (see Dart, '40). A long list of Bush infantile features has been given recently (Tobias, '57). Among the features enumerated is the strong bossing of the vault-bones. In its powerful frontal, parietal and occipital bosses, the Bushman cranium could be said to have carried forward its juvenile morphology into adulthood.

A totally different approach to the subject has been proposed by the present author. Instead of looking upon the neotenous phenomena as a kind of teleological manifestation, I have suggested that the variations in morphology be regarded as the effect of gene mutations (probably coupled with environmental effects) altering the rates of differentiative processes. We know that most genes act by influencing the direction, timing or rate of phenogenetic and morphogenetic processes. So it is not inconceivable that gene-mutations may have occurred which retarded certain differentiative processes: moderate retardation would lead to the late appearance of morphological features; marked retardation might result in a gene-product or organizer appearing too late to take effect, i.e., after its phenocritical period, so that a morphological feature might fail to appear. On the other hand, accelerating mutations might speed up differentiative processes and result in the early appearance of adult morphological traits. An infantile morphology, on this view, would result from a series of retarding mutant genes, which might have become selected by conferring slight advantages on the bearer. It is in the light of this genetic conception that the further discussion is couched.

The phenotypic characters resulting from retarded differentiation include, as we have seen, the degree of bossing of the vault-bones, as well as other easily detectable cranial features. If, now, we were to examine fossil crania, reasonably believed on morphological and archaeological grounds to be antecedent to the Bushman, we should be in a position to detect at what point in time the retarding mutations became manifest. Based on this line of reasoning, I have elsewhere suggested that the Bushman stemmed from essentially adultiform ancestors, as represented by the big-browed "Rhodesioid" group (Broken Hill, Saldanha, Florisbad, Lake Eyassi) and that the retarding mutations began before the end of the Middle Stone Age (Tobias, '55–'56, '56, '57). The earliest indications of such a tendency are perhaps the diminution and indentation of the upper facial (maxillary) skeleton of Florisbad man, (whose parietal and occipital bosses
are, however, lost to us) and the mass
bossing of the Singa cranium.

In a previous paper (Tobias, '59a)
was suggested that, whereas sutu
growth of the cranium was predomin
and appositional growth relatively un
portant in thin-skulled forms like mod
man, in human types like Rhodesian M
with heavy bony excrescences, such as
bital and occipital tori, appositional grow
of bone must be correspondingly more
portant. The result of such appositio
growth in the occipital region is that
arc from lambda to opisthion is relativ
lengthened, without corresponding chan
in the chord, and a lower occipital inc
follows. If in figure 1 we examine
occipital contours of Rhodesian Man w
his heavy torus and of a Bush crani
with smooth occiput, we see that an id
tity of occipital index may result fr
two apparently different processes: first
in Rhodesian Man, heavy appositio
growth together with a well-curved occi
tal, and secondly, in a Bush cranium, o
marked curvature of the occipital, mould
by sutural growth mechanisms to the co
tours of the underlying brain. In the e
lutionary raising of the occipital ind
two processes therefore come about, t
elimination of most appositional grow
i.e., of the occipital torus, and the flatte
ing of the basic curvature of the occipi
bone. Cappieri ('57), in a recent disc
sion of the development of the mode
rounded form of the calvaria, has reco
nized two phases, a first in which the cra
ial base has decreased and the vault b
come more rounded, and a second
which the torus orbitalis and torus occi
talis are decreased. While this may be t
sequence of events in Caucasoid popu
tions (and Cappieri's discussion aris
from a description of "protomediterranea
skulls), in the African sequence it wou
seem that the order of events was reverse
For while our living Bushmen have lost a
most all trace of the bony prominence
they have retained angular, unround
crania with extreme occipital curvature

It emerges from this study that the r
tarded differentiation of the Bush craniu
has arisen in a series of stages, the first
which goes back to the beginnings of ma

self. At the stage of human emergence, only the occipital bone which remains arkably fetal in form throughout life. is a fundamental fetalizing change nguishing hominids from pongids. A occipital with no other fetal features e cranial vault characterizes *Australo-ecus, Pithecanthropus, Homo neanhalensis* and *Homo rhodesiensis*.

he second stage in the retardation ess affects the differentiation of the etal bones, as exemplified best by the *a* cranium. In this cranium, the occi-. is markedly protuberant (Oc.I. 55.4) mbling, as Wells ('51) comments, the ipital contour of many Bush skulls. wise the parietal bosses are exception- prominent, lying at the center of a e of very obvious radially-orientated e trabeculae. In other words, the dif-ntiation of the parietals has been re-ed, presumably in conformity with a istribution of underlying brain sub-ce. Hence, we see retarded morpholog- differentiation in both occipital and etal regions. The frontal and facial ons, however, show exactly the oppo- The forehead is low and sloping; e is a powerful orbital torus; the orbits long and the structure of the zygomatic e at its insertion behind the torus is iniscent of a robust, palaeoanthropic gerontomorphic strain such as that of ken Hill. There is thus a marked dis-ty between the anterior and posterior s of the cranium: the posterior mani-ing retarded differentiation, the an-or showing non-retarded development. nother example of this type of skull is of *Istrice* studied by the author in the yndon Museum, Nairobi. Here, too, we e a frankly Bushmanoid (retarded) lt and a discordantly adultiform fore-d and face, a type of morphology which ms to have survived at least to fairly ent times.

he third stage is marked by the exten- forwards to the frontal and facial re-ns of the tendency towards retardation. h the final sweeping of these regions ler a retarded controlling mechanism, completely infantile, pentagonoid vault erges, as in the Cro-Magnon, Boskop Bushman skulls. In Southern and Central-East Africa, this must have taken place before the end of the Middle Stone Age, to give rise to the Boskop and Bush physical types.

We might recognize a fourth stage in occipital evolution, whereby a flattening sets in, in the emergence of some strains of modern man, especially the Negro. Since we have no planoccipital fossil crania of any considerable antiquity, it seems certain that the Negro cranium must have developed from a curvoccipital ancestral cranium. Unfortunately, in contrast with the Bushman, we have no long lineage of proto-negroid fossils to corroborate this hypothesis in relation to the Negro. The postulated phylogenetic flattening of the occipital, which we have shown is recapitulated in each modern Negro ontogeny, is presumably brought about by accelerating mutations. In other races, which have retained the curvoccipital cranium, it may be supposed that these accelerating and differentiating changes did not occur. Here it may be interpolated that, in accordance with recent studies on skull growth, the mutations we are referring to probably applied more directly to the underlying brain growth and only by secondary intention to the bones of the encapsulating vault (Tobias, '59a).

We see now that the big occipital bosses of the Bushman are not of the same morphological or taxonomic valency as the parietal bosses; the occipital boss has been there, the evidence would suggest, since the days of *Australopithecus*, whereas the parietal bosses are part of a rather late retarding specialization.

SUMMARY

1. All early fossil hominid crania, both African and non-African, have ultra-strong occipital curvature.

2. On its occipital indices, *Australopithecus prometheus* falls with the Hominidae and, more particularly, with the more ancient types of man from Africa.

3. In North Africa, the earliest crania to show some degree of occipital flattening are those of Mechta, Afalou and Asselar (Late Palaeolithic).

4. In East Africa, the earliest crania showing some occipital flattening are those

from a variety of Kenya Smithfield, Mesolithic and Neolithic sites.

5. In Southern Africa, the earliest crania to show occipital flattening are those from the Wilton (Later Stone Age) level at Matjes River.

6. Among non-African forms, appreciable flattening of the occiput does not manifest itself until late in the Upper Palaeolithic.

7. Of all adequately studied cranial series anywhere in the world, the Bushmen alone among modern races has preserved the extreme occipital curvature of fossil man.

8. Since the highly curved occipital of the adult Bushman represents, too, the retention of an infantile characteristic into adulthood, it is suggested that the occipital curvature of the Bush cranium is the result of genetically retarded differentiation.

9. Infantile morphology or retarded differentiation of the cranial vault has arisen in three stages: (a) Initially, only the occipital bone remains remarkably fetal in form throughout life, as in *Australopithecus, Pithecanthropus, Homo neanderthalensis* and *Homo rhodesiensis*. (b) Retarded differentiation "moves forward" to affect the parietal bones as well, as in the Singa cranium. (c) The frontal region is engulfed by the wave of retarded differentiation, giving the completely infantile form of the cranium, as in Cro-Magnon, Boskop and Bushman.

10. A fourth stage in occipital evolution, whereby a flattening sets in, marks the emergence of some strains of modern man, especially the Negro.

11. Occipital and parietal bosses are of very different taxonomic valency, the occipital bulge having been present since the dawn of man, the parietal boss being part of a rather late retarding specialization.

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Blood Group Genes of the Copper Eskimo[1]

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is report deals with the blood group ecretor genes of the so-called Copper ıo living on Victoria Island and the boring mainland, roughly between and 120° west latitude and from the : Circle to 72° north longitude. The t is part of a continuing study under egis of the National Museum of Can- of the populations which go to make e population of Canada.

e Copper Eskimo form an almost bred population of about 1000 which een stationary as to numbers since were first studied by Jenness ('23) in –16. Where they came from and long they have lived here is unknown. caribou and seal were their main- , providing food, clothing, fuel and ng materials, while in their territory ıative copper which they used both for ıfacture and for trade. Neither the nor the west offered greater attrac- , while the south was barred by Atha- ın-speaking Indians. It seems prob- that they have occupied their present ory for a long time. On the other it is not to be imagined that they in complete isolation. Their neigh- 300 miles to the west about the delta e Mackenzie knew of them, but only ; they spoke of them as "the people off." To the east and southeast they ome slight contact with other Eskimo, ındoubtedly there was some intermar- . With the Indians to the south they apparently in a constant state of of small raids of extermination. So arliest record we have of them is in ıel Hearne's journal of his journey Fort Prince of Wales on Hudson Bay e mouth of the Coppermine River in : in that venture the Indians who npanied Hearne killed every Eskimo encamped. Even so, from tales we told, it is reasonable to believe that ıer raids an occasional Indian woman or child may have been spared and incorporated into the population.

As to the other admixtures there was only a rare contact between Eskimo and people other than Indian from 1771 until about 40 years ago. These were not whaling waters. A few explorers and trades entered the area, some of whom married Eskimo women. These events are so recent that children of these marriages are still living, a number of whom we tested. Today there are two small white settlements, that at Cambridge Bay and that at Coppermine, and several still smaller implants.

In the present study 330 out of the total of approximately 1000 were tested. With the help of Corporal and Mrs. D. McDougal of the R.C.M.P., Father LaPointe, O. M. and the Reverend Canon Sperry a detailed genealogy was drawn up. There were no first-cousin marriages.[3] The genealogy could not be carried far enough back to prove or disprove second-cousin marriages. Of the 330, only 10 could be proved to have white ancestors; these 10 were eliminated in gene frequency analysis. Such analysis was carried out for the remaining total 320 and for 46 among them who were apparently unrelated. While there is no significant difference between the two estimates, we think analysis based on the 320 is probably more accurate since phenotypes of low frequency were then represented. The estimates in the tables are so based. There is a high death rate in young adults, so it was unusual to obtain blood from children and both parents. Few genotypes could therefore be defined but in what family data we did obtain, there was no disagreement between expected phenotypes and those found.

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[1] Assisted by a grant from the National Museum of Canada. Dr. Jacques Rousseau, Director.

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[3] See addendum.

SAMPLES, SERA AND METHODS

Samples were collected at Cambridge Bay, Holman Island, Reid Island and Coppermine in April, 1958 and the tests carried out at the Hudson's Bay Company post at Coppermine. With the exception of the specimens from Cambridge Bay (which were venous samples obtained for us by Dr. Gillison of the Department of National Health, sent by air to Coppermine and tested on the third day) all samples were of capillary blood taken into saline and tested on the day of collection.

The test sera had all been in use in our laboratory for some time so that their specificity and mode of action were well known. We had taken test cells of various known antigen constitution with us; these were used daily to control the results. Five methods were used according to the mode of action of the various sera; agglutination in a capillary tube by untreated serum (Chown and Lewis, '51) indicated below by "capillary;" agglutination in a capillary tube by serum mixed with activated papain (Lewis et al., '58) indicated below by "capillary papain;" the indirect Coombs technique of Race and Sanger ('58) modified to the extent that the final agglutination with anti-human-globulin rabbit serum (Coombs' reagent) was carried out in a capillary tube, indicated by "indirect Coombs;" agglutination in bovine albumin (Lewis and Chown, '57), indicated below by "short albumin;" open well slide, so stated below. In the following the serum is described first; the method is given after the semicolon. The letters in brackets are our code names for the particular serum used. Unless otherwise indicated tests were made at room temperature which varied from 18° to 22°C.

The ABO system. One each, high titre, avid anti-A and anti-B and one anti-A + B from O donor; capillary. One commercial anti-A$_1$ (absorbed B); open well slide.

The MNSs system. One commercial anti-M; capillary. One commercial anti-N; open well slide. One anti-S (Dev), one anti-s (Chei); capillary. One anti-Mi^a (UB no. 4), one anti-M^g (HA1); capillary. One anti-Vw(Gill); short albumin. One anti-He (Sha); open well slide.

The P system. One anti-P (Wil); c
lary at refrigerator temperature. One
ti-Tj^a(Ell); capillary.

The Rh system. One each anti-C
(comm.), anti-C^w(Bosh), anti-D (F
capillary. One each anti-c (Tod), a
(McL), anti-e (Hal); capillary papain
further anti-c (Gai), anti-E (Ros),
anti-e (Sha) for those samples reacti
CcDee or ccDEe; capillary papain.
every case the reaction with the c
serum agreed with the reaction obta
with the primary test serum.) One a
(Ros); indirect Coombs.

The Lutheran system. One each
Lu^a(TG) and anti-Lu^b (TG); capillar

The Kell system. One each anti-K (N
anti-k (Ort); capillary papain. One
anti-Kp^a(97B) and anti-Kp^b + K (Ra
indirect Coombs.

The Duffy system. One anti-Fy^a (
and one anti-Fy^b (Mul); indirect Coo

The Lewis system. One anti-Le^a (M
capillary.

Other systems. One anti-Wr^a (S
capillary at 37°. One each anti-Di^a(W
anti-Be^a, anti-By^a, anti-Yt^a (Cart); ind
Coombs.

Secretor status. Saliva samples wer
luted one part to one part of saline, he
in a boiling water bath for 10 min
centrifuged and the supernatant te
all of groups A, B and AB being teste
inhibition of anti-A, anti-B and anti-H
of group O for inhibition of anti-H (Ul
There were no discrepancies as betwee
hibition of anti-A or B and anti-H, w
since all proved to be secretors, the in
tion tests served to confirm the b
grouping.

RESULTS

The results are set out in table 1 t
The gene frequencies for the MN, Ss
Rh groups were determined by gene co
the others by square root methods o
in the case of MNSs, by a combinat
Those of group O who were P-nega
were tested with anti-Tj^a and were posi
Hence, in that system, the frequencies
based on an assumed absence of *p*. O
than this the tables are self-explanator

TABLE 1

The ABO system

Phenotype	Number	Frequency observed	Frequency expected	Number expected	Gene frequencies
O	146	0.4563	0.4583	146.66	O 0.6770
A_1	153	0.4781	0.4794	153.41	A_1 0.2914
B	14	0.0437	0.0438	14.02	B 0.0316
A_1B	7	0.0219	0.0184	5.89	
Totals	320	1.0000	0.9999	319.98	1.0000

TABLE 2

The MN system

Genotype	Number	Frequency observed	Frequency expected	Number expected	Gene frequencies
MM	221	0.6906	0.7092	226.94	M 0.8422
MN	97	0.3031	0.2659	85.09	N 0.1578
NN	2	0.0063	0.0249	7.97	
Totals	320	1.0000	1.0000	320.00	1.0000

TABLE 3

The Ss system

Genotype	Number	Frequency observed	Frequency expected	Number expected	Gene frequencies
SS	14	0.0437	0.0334	10.69	S 0.1827
Ss	89	0.2781	0.2987	95.58	s 0.1873
ss	217	0.6782	0.6679	213.73	
Totals	320	1.0000	1.0000	320.00	1.0000

TABLE 4

The MNSs system

Phenotype	Number observed	Frequency observed	Frequency expected	Number expected	Gene frequencies
MMSS	14	0.0437	0.0295	9.44	
MMSs	67	0.2094	0.2304	73.73	MS 0.1719
MMss	140	0.4375	0.4493	143.78	Ms 0.6703
MNSS	0	0.0000	0.0000	0.00	NS 0.0000
MNSs	22	0.0687	0.0543	17.38	Ns 0.1578
MNss	75	0.2344	0.2116	67.71	
NNSS	0	0.0000	0.0000	0.00	
NNSs	0	0.0000	0.0000	0.00	
NNss	2	0.0063	0.0249	7.97	
Totals	320	1.0000	1.0000	320.01	1.0000

TABLE 5

The P system

Phenotype	Number	Frequency	Gene frequencies
P+	107	0.3344	P_1 0.1842
P−	213	0.6656	P_2 0.8158
Total	320	1.0000	1.0000

TABLE 6

The Rh system

Phenotype	Number	Frequency observed	Frequency expected	Number expected	Gene frequencies
CCDee	81	0.2531	0.2485	79.52	
ccDEE	78	0.2437	0.2407	77.02	*CDe*(± *Cde*) 0.4985
CcDEe	154	0.4813	0.4891	156.51	*cDE*(± *cdE*) 0.4906
CcDee	3	0.0094	0.0109	3.49	*cDe*(± *cde*) 0.0109
ccDEe	4	0.0125	0.0106	3.39	
ccddee } ccDee }	0	0.0000	0.0001	0.03	
Totals	320	1.0000	0.9999	319.96	1.0000

TABLE 7

The Duffy system

Phenotype	Number	Frequency	Gene frequencies
Fy(a+)	300	0.9375	Fy^a 0.7500
Fy(a−)	20	0.0625	Fy^b 0.2500
Totals	320	1.0000	1.0000

TABLE 8

Other systems

System	Phenotype	Number tested	Frequency
Lutheran	Lu(a−b+)	146	1.00
Kell	K−k+Kp(a−b+)	320	1.00
Lewis	Le(a−)	299	1.00
Secretor	Secretor of appropriate A, B, or(and) H substance	200	1.00
	Yt(a+)	146	1.00

TABLE 9

Antigens apparently lacking (i.e., not demonstrated)

System	Antigen	Number tested (all negative)
MNSs	He	320
	M^g	320
	Mi^a	320
	Vw	146
Rh	C^w	320
	V	320
Diego	Di^a	320
Berens	Be^a	88
Batty	By^a	299
Wright	Wr^a	299

DISCUSSION

The gene frequencies of this population are in some ways similar to, and in others different from, those of other Eskimo populations that have been studied. As to similarities there is, as in others, a low frequency of P_1, absence of K, of Le^a and of Di^a, and a high frequence of cDE. As to differences there are three of note. In the ABO system the frequency of (0.0316) is low in comparison with that of the Eskimo of Alaska and southern Greenland, but is little if at all different from the frequency along the coast of Hudson Bay. In the Duffy system we proved by direct test the presence of Fy^b in the population and assume that it contains only the two Duffy genes Fy^a and Fy^b . On this basis the frequency of Fy^b is higher than in other populations we have tested. In the MNSs system the Copper Eskimo have the highest frequency of MS and the lowest Ns of any group we have examined. Judging by the following tentative frequencies there are

to be a cline from northwest to south- MS being replaced by Ns:

ion	MS	Ms	NS	Ns
.	0.1719	0.6703	0.0000	0.1578
Iudson	0.1524	0.6090	0.0000	0.2386
Island	0.1200	0.5943	0.0000	0.2857
ast son Bay	0.1337	0.5646	0.0000	0.3017
ast son Bay	0.0619	0.5662	0.0000	0.3719

e meaning of these differences is un- n. The ABO findings taken alone be used as evidence supporting the nent that the Eskimo living farthest in Hudson Bay have a large admix- f Indian blood; indeed to the absurd- at they are pure blood Indians. But the Duffy and the MNSs data destroy rgument. In point of fact so far as NSs data go the closer geographically skimo come to the modern Indians rther they recede from them geneti- It would seem to us that, as more lete blood groups and other genetic accumulate, one can but conclude there is no close genetic relationship een the Eskimo and the Indians of . They may perhaps stem from a non stock, but if so the primary hing occurred a long, long time ago, there has been little grafting since. lly in our own studies there is sur- gly little evidence for replacement of no genes by genes of Whites. Such resent certainly, but not in such num- n the populations we have studied as sly to disturb the inherent Eskimo frequencies. If neither of these is xplanation of the variations then that nation must lie within the Eskimo ation itself.

e archaelogists have painstakingly de- at least two Eskimo cultures in the n Arctic, the Dorset and the Thule. uld seem to us not unlikely that eople of these cultures differed genet- , perhaps as much as the Indians of do from the Eskimo, and that there may well be in the present Eskimo population a Dorset residuum which is genetically recognizable. It is hardly to be expected that such recognition will depend upon the presence of a strange gene in one population that is absent from the other, but rather upon differences of frequencies of genes already known or to be discovered, differences such as are indicated in the above data. One can as yet draw no firm conclusions, but certainly the indications are enough to make further genetic studies, even more complete than the present one, worth-while.

SUMMARY

Blood group gene frequencies were determined based on samples from 320 Copper Eskimo as follows: *O*, 0.6770; A_1 0.2914; *B*, 0.0316; *M*, 0.8422; *N*, 0.1578; *S*, 0.1827; *s*, 0.8173; *MS*, 0.1719; *Ms*, 0.6703, *NS*, 0.0000, *Ns*, 0.1578; P_1, 0.1842, P_2, 0.8158; *CDe*(±*Cde*), 0.4985; *cDE*(±*cdE*), 0.4906; *cDe*(±cde), 0.0109; Fy^a, 0.7500; Fy^b, 0.2500. The following phenotypes were found to have a frequency of 1.00; Lu (a − b +), K − k + Kp(a − b +), Le(a−) and Sec. The following antigens were not present in the population tested: He, M^g, Mi^a, Vw, C^w, V, Di^a, Be^a, By^a, and Wr^a. Differences between this population and other Eskimo populations studied were noted in the ABO, MNSs and Duffy systems.

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ADDENDUM

Since this article was written we have obtained additional genealogical information from Mr. Wm. Joss, Manager of the

Hudson's Bay Company post at Reid Island, who obtained much of it from Ageak, an Eskimo of some 70 or more years. Four out of 60 matings in the most recent major mating generation were between first cousins. We are deeply indebted to Mr. Joss and to Ageak for the great care with which they went into this question for us.

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ısity of Cervical Vertebrae and Comparison with ısities of Other Bones[1]

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is believed that femora and humeri a greater proportion of compact bone ve to cancellous than do vertebrae; femora and vertebrae are subjected ɔre compressive force because of their ıt-bearing role than are humeri whose :ion subjects them to greater tensile compressive force; and that the more ally the vertebrae are located the er is the compressive force since a er weight is borne (Evans, '57). ıermore, there is evidence to suggest the density of the skeleton varies ac- ng to race and sex and that the den- is reduced with aging.

ıis paper will present data pertaining ıe density of the cervical vertebrae skeletons of both sexes of two races with a wide age range, and compari- will be made with the densities of ra and lumbar vertebrae (Broman, :er and Peterson, '58) and humeri tter, Broman and Peterson, '58) of ame skeletons.

MATERIAL AND METHOD

series of 80 skeletons, equally divided een each sex and between American :es and Negroes with approximately same age range constitutes the ma- l. The details of source and prepara- are recorded elsewhere (Trotter and rson, '55). The bones were weighed in the dry, fat-free state. The volume was taken of each series of cervical vertebrae by displacement of millet seed in a 1000-cm^3 graduated cylinder with the bones simulating the anatomical position. The technique differed only in the size of the cylinder from that for femora and lumbar vertebrae where the size was 4000 cm^3 (op. cit.) and from that for humeri where it was 2000 cm^3 (op. cit.). It is advantageous to utilize a cylinder of the smallest size which will accommodate the bones. As in the earlier studies the per cent error of the method was determined from two measurements each of 10 series of vertebrae chosen at random and for the cervical vertebrae the error was found to be 1.0%.

The statistical procedures were selected and carried out by Barbara Bartels Hixon, to whom grateful acknowledgment is made.

Density of cervical vertebrae

The mean age of the skeletons and the mean weight, volume and density of the cervical vertebrae for each of the 4 groups are presented in table 1.

The differences in the mean ages are not large, nevertheless the Whites are older than the Negroes. As expected the mean weight, volume and density are greater in Negroes than in Whites and in males than in females.

Differences among group means. An analysis of variance of the differences among the group means is as follows:

Source of variation	Degrees of freedom	Mean square	Variance ratio (F)	P
Among 4 group means	3	0.0682	7.29	< 0.001
Male vs. female	1	0.0775	8.28	< 0.01
Negro vs. White	1	0.1224	13.08	< 0.001
Interaction	1	0.0047	< 1	
Within groups (error)	75[1]	0.0094	1	

[1] In this and succeeding analyses one degree of freedom was lost from the error term because of a substitution in the White male group by missing plot technique.

[1] ɹpported by grant A-1013 M & N, U.S.P.H.S.
[2] ımmer Research Fellow, 1955–57.

TABLE 1

Means and standard deviations (S.D.) of age (years), weight (gm), volume (cm³), and density (wt./vol.) of cervical vertebrae according to race and sex

Group	No.	Age		Weight		Volume		Density	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
White male	20[1]	64.0	12.8	53.9	9.3	104.9	12.8	0.517	0.065
Negro male	20	59.6	13.9	59.0	13.2	101.6	14.8	0.580	0.090
White female	20	67.2	17.1	37.6	9.6	86.0	13.8	0.440	0.102
Negro female	20	60.3	19.8	46.4	10.1	88.2	14.2	0.533	0.121

[1] In two skeletons of the White male series the cervical vertebrae had been sacrificed for another study. For one a value based on a skeleton of comparable age, race and sex was substituted; for the other a substitute value was derived by the missing plot technique (Snedecor, '56, 5th ed., p. 310), since no comparable skeleton was available.

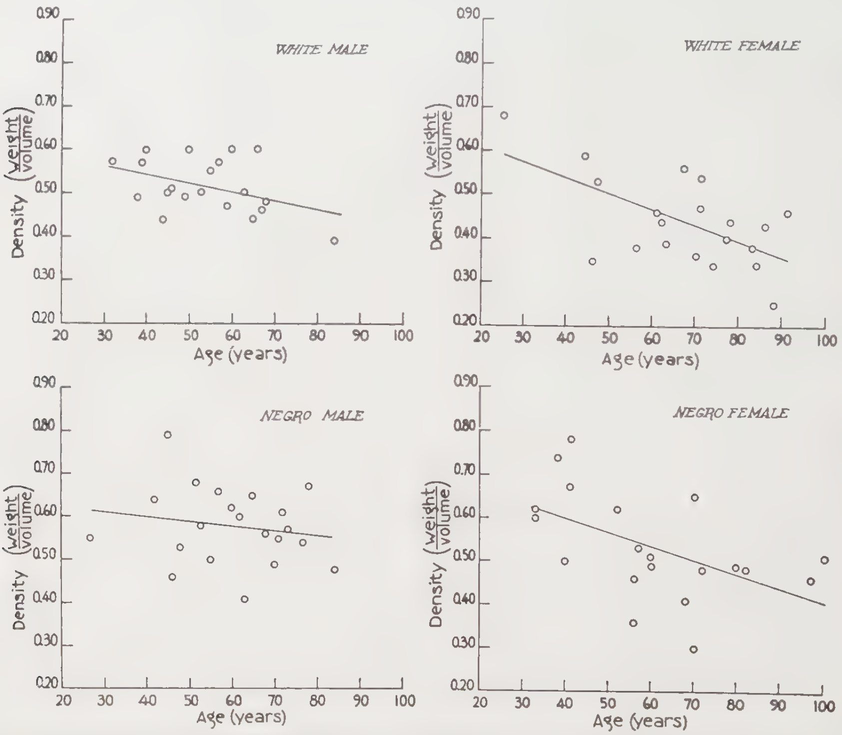

Fig 1. Scattergrams and regression lines of density on age of cervical vertebrae for each sex-group.

It is seen that the differences among the 4 group means are highly significant ($P < 0.001$) and that these differences are accounted for by both sex and race since the variance ratio for each is significant.

Effect of age. In figure 1 are shown the densities of cervical vertebrae plotted against age and the regression line of each of the 4 groups.

The calculated slopes are as follows:

Group	Slope	P
White male	–0.0021	n.s.
Negro male	–0.0010	n.s.
White female	–0.0036	< 0.01
Negro female	–0.0032	< 0.05

The densities of each group decrease with age but only in the two female groups do the calculated slopes significantly differ from zero.

:est of parallelism of the regression ,of the 4 groups indicates that the ined slope is significantly different zero ($P < 0.001$) and that the indi-l slopes do not differ significantly the best fitting combined slope with ivergence among the 4 slopes being han the error term, i.e., the scatter id the separate slopes.

ferences among group means after tment for differences in age. By the sis of covariance in which correction fferences in age is made, it is shown he variation found among the mean ties of the cervical vertebrae of the ups by the analysis of variance is still nt and accounted for by both sex and The only difference in the levels of icance found in the two analyses is between the races, whereby correction fferences in age altered the probability from less than 0.001 to less than 0.01. either analysis was the interaction l to be significant. The analysis of iance is shown as follows:

ource of ariation	Degrees of freedom	Variance ratio	P
g 4 groups	3	6.32	< 0.001
e vs. female	1	8.59	< 0.01
ro vs. White	1	10.25	< 0.01
raction	1	< 1	n.s.
n groups (error)	74	1	

omparison of densities of cervical vertebrae, lumbar vertebrae, humeri and femora

e findings pertaining to the last three of bones may be found in the earlier ts (op. cit.).

ferences among means of sex-race s for each bone series. The means standard deviations of each series of bones according to sex and race are summarized in table 2.

The densities within each sex-race group are seen to be higher in the long bones, humeri and femora, than in either series of vertebrae. The long bones have a greater proportion of compact to cancellous bone than have the vertebrae. Likewise, in the same sex-race group the densities are higher in the cervical vertebrae than in the lumbar vertebrae, the former having a greater relative amount of compact bone. For each group of bones higher densities are found in males than in females and in Negroes than in Whites.

Differences among means of sex-race groups before and after adjustment for differences in age. The differences among the mean densities for any one series of bones of the 4 sex-race groups have been found to be significant by the analysis of variance. After adjustment was made for differences in age the probability levels remain the same except for the femora which are found to be not significant. In table 3 are summarized the levels of significance of differences in densities and of the sources of the variation for each series of bones before (analysis of variance) and after (analysis of covariance) correction for differences in age was made.

For each bone series the degrees of freedom were subdivided into one each for sex, race and interaction. Differences attributable to sex are significant only among the cervical vertebrae and humeri and this finding is not altered by adjustment for age differences. On the other hand, differences attributable to race are significant for each group of bones, although at different levels of probability; but, after adjustment for age differences, the level of

TABLE 2

Summary of means and standard deviations (S.D.) of densities of 4 groups of bones from the same series of skeletons

	Cervical vertebrae		Lumbar vertebrae		Humeri		Femora	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Vhite male	0.517	0.065	0.408	0.098	0.642	0.113	0.628	0.114
Jegro male	0.580	0.090	0.483	0.097	0.718	0.102	0.700	0.087
Vhite female	0.440	0.102	0.380	0.080	0.566	0.114	0.598	0.121
Jegro female	0.533	0.121	0.458	0.141	0.640	0.139	0.652	0.129

TABLE 3

Summary of levels of significance of mean differences by the analyses of variance and covariance for each series of bones and for the contributions to the differences by sex, race and interaction of the two

	Analysis of variance (no adjustment)				Analysis of covariance (adjustment for age)			
	Cervical vertebrae	Lumbar vertebrae	Humeri	Femora	Cervical vertebrae	Lumbar vertebrae	Humeri	Femora
Among 4 groups	< 0.001	< 0.05	< 0.01	< 0.05	< 0.001	< 0.05	< 0.01	n.s.
Male vs. female	< 0.01	n.s.	< 0.01	n.s.	< 0.01	n.s.	< 0.01	n.s.
Negro vs. White	< 0.001	< 0.01	< 0.01	< 0.05	< 0.01	< 0.05	< 0.05	n.s.
Interaction of sex and race	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

ility is reduced for each group and case of the femora the differences are ger significant. The interaction of d race is found to make no significontribution to the differences among ean densities of any of the 4 series es. Thus, it is seen that the cervical rae and humeri, the bones with less -bearing function, show greater dif- es in density among the sex-race than do lumbar vertebrae and a, the bones with greater weight- g function.

erences among mean densities of the es of bones within each sex-race The densities of the 4 series of within each of the 4 sex-race groups keletons in each group) were tested gnificant differences by the analysis iance. The differences are found to hly significant ($P < 0.001$) in each

three degrees of freedom among the es of bones in each group have been ed to:

The more compact bones, humeri and a, vs. the less compact bones, cervical mbar vertebrae;

The more weight-bearing bones, lum- ertebrae and femora, vs. the less t-bearing bones, cervical vertebrae umeri; and,

Interaction between 1 and 2, i.e., ure vs. function.

interaction is significant ($P < 0.01$) ch group showing that the density lumbar vertebrae does not corre- to the density of the femora in the way that the density of the cervical rae corresponds to the density of the ri. Inspection of the mean densities e bones in each of the 4 sex-race s (table 2) shows that the difference en the densities of cervical vertebrae umeri is not as great as that between ties of lumbar vertebrae and femora ch group. Since the interaction in group is significant, over-all compariwould be of little value. Therefore, idual comparisons were made through daptation of Tukey's method (Sne- , 5th ed., p. 251) in which the dif- ce between the mean densities of wo series of bones within each group mpared with a calculated significant difference. The difference between the densities of each combination of any two series of bones was found to be significant ($P < 0.01$) in every case except for the difference between the densities of humeri and femora which is not significant for any sex-race group. Thus, of the 4 bones the two which are most alike in structure and least alike in function do not differ significantly in density.

Effect of age. The calculated slope of the densities of each series of bones with age in each sex-race group is negative, indicating a decrease of density with age (fig. 2). The slope is significantly different from zero except for the cervical vertebrae in the two male groups and for the lumbar vertebrae in the Negro male group. Since all slopes are negative it is possible that larger samples of these groups would provide regression coefficients which are significant, also. The linear or straight line regression of density for the combined series of the 4 bones with age in each of the 4 sex-race groups is significantly different from zero ($P < 0.001$), but the scatter about the line is also highly significant ($P < 0.001$ for each), indicating that some type of curve might be a better fit than a straight line although no particular type is apparent from the scattergrams. When all 16 slopes are compared there is no indication of departure from parallelism, i.e., all slopes could have been obtained by random sampling from the same bivariate population. Thus, it appears that density is reduced with age uniformly in each of the 4 series of bones in each sex-race group.

SUMMARY AND CONCLUSIONS

The densities (weight/volume) of the cervical vertebrae from 80 adult skeletons were determined and compared with the densities of the lumbar vertebrae, humeri and femora from the same skeletons. The skeletons were derived equally from American Whites and Negroes of both sexes, each group with a wide age range. Weight was taken of the bones in a dry, fat-free state; volume was measured by displacement of millet seed.

It was found that:

1. The mean density of cervical vertebrae is significantly greater in Negroes

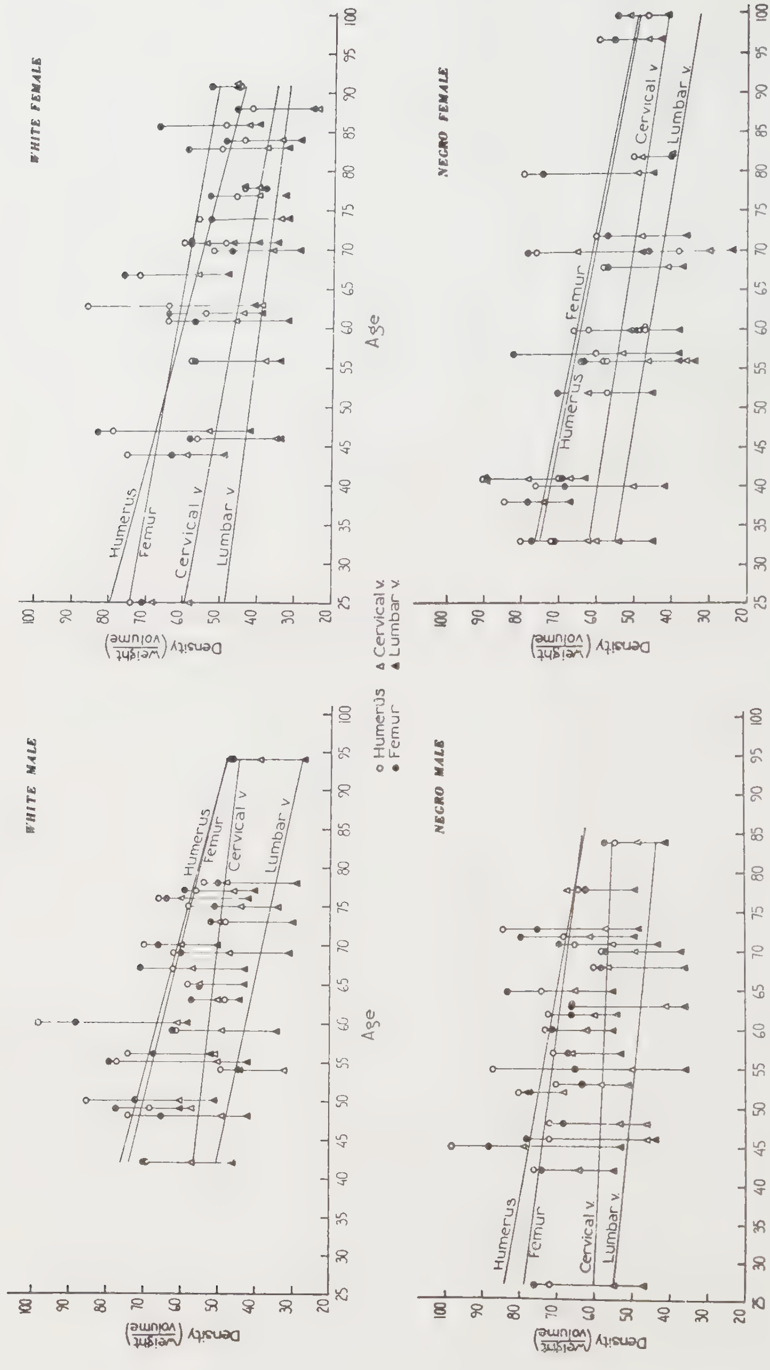

Fig. 2 Scattergrams and regression lines of density on age of 4 series of bones from each skeleton (indicated by vertical line) for each sex-race group.

n in Whites and in males than in ıales.

;. The densities of cervical vertebrae of h sex-race group decrease with age, but y in the female groups are the slopes ıificant.

. After correction for age differences ɔng the 4 sex-race groups the mean sities of each series of bones except of ıora differ significantly. In the cervical :ebrae and humeri the difference is ·ibutable to sex (male bones denser than ıale) and to race (Negro bones denser n White), whereas in lumbar vertebrae y race plays a significant part.

·. The mean densities of the 4 series ɔones within each sex-race group differ ıificantly. There are significant differ-es between any two series of bones ex-t between humeri and femora.

;. The densities of each series of bones each sex-race group are found to de-ase uniformly with age; apparent dif-ences in slope are accounted for by ıpling variation. The combined slope l all except three of the 16 regression fficients (of cervical vertebrae for the ı male groups and of lumbar vertebrae for the Negro male group) are significantly different from zero.

Thus, from this study of the 4 series of bones, it is concluded in general that bones of the Negro skeleton are denser than those of the White skeleton; that less weight-bearing bones (cervical vertebrae and humeri) of the male are denser than those of the female and that for the more weight-bearing bones (lumbar vertebrae and femora) the role of sex is not so marked; that bones which are alike in structure although unlike in function (humeri and femora) do not differ significantly in density; and that bone density decreases with age.

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e Inconstancy of Physique in Adolescent Boys d Other Limitations of Somatotyping[1]

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central problem in somatology is the e and definition of the more invari- "constitutional" characteristics of the ing organism. The present study of problem is based chiefly on nude, full- th photographs of 71 White adoles- boys. It is a continuation of a study Hunt, Cocke and Gallagher ('58), in h somewhat distinctive chronologies exual maturation were found in boys ifferent somatotypes.

nce this previous study was wholly s-sectional, our newer work has used ly longitudinal data. The physique of y at pubescence can thereby be com- d with his subsequent maturation, and aturity with his antecedent pattern of al development. Equally important is continuity or predictability of body d during adolescence. We have inves- ted this continuity by means of photo- hic assessments by the senior author nt). Since Hunt's ratings are some- t idiosyncratic, their agreement with lar evaluation by other experienced kers is reviewed by means of factor lysis. In general, our evidence adds to theoretical and technical limitations hotographic ratings of physique, some vhich have already been discussed by er, Hunt and Sen ('58).

Selection of the adolescent series

he adolescents in our study were pho- aphed in Oakland, California during ngitudinal investigation under the di- ion of Dr. Herbert R. Stolz. Many of somatological findings on the growth his sample have been ably described monograph by Stolz and Stolz ('51). s volume also contains some of the tographs whose originals we evaluated.

The serial photographs of each boy usually begin at 10–11 years of age, and are repeated at intervals of about 6 months to a maximal age of about 17 to 18 years. At each age, a trio of standing photographic views is available: front, side and rear.

At all ages, the junior author rated sexual maturation from the photographs, using the standards of Tanner ('55). This part of the study was completed prior to his training or reading in somatotyping. The senior author then independently rated the physique of each boy at extreme ages dictated mainly by the individual's own period of serial study. This separation of ratings of physique and sexual maturation was designed to reduce bias in comparing the two phenomena.

The chief criterion for selecting the present sample was that at least one trio of photographs be available at or beyond 16.5 years of age. In each case, the oldest trio was rated, and nearly all were at either 17 or 18 years old. The whole series of older photographs is defined as the "subadult" age group, since all of the boys had reached Tanner's final stage of adolescent maturation of the genitalia and pubic hair (stage 5).

For each member of the "subadult" group, an earlier trio of photographs was chosen at the age nearest to 11.5 years. At this younger age, 31% of the boys had attained or surpassed the onset of adolescent enlargement of the testes. Serial skinfold measurements with the Franzen caliper on nearly all of these boys showed that about 80% had not yet reached the maximum adipose thickness of their "fat spurt"

[1] The research reported herein was supported in part by research grant A-1372, U. S. Public Health Service, National Institutes of Health.

(Stolz and Stolz, '51). In their younger photographs, then, most of the boys were almost pubescent, and these pictures are therefore designated as the "prepuberal" age group.

Ratings of physique

Most workers today who rate physique from full-length photographs are the bearers of a cultural tradition based largely on the work of Sheldon and his associates ('40, '42, '49, '54). Enough disagreement now exists, however, so that it is desirable to mention how the present ratings of adolescent boys were carried out.

Hunt, who performed these assessments, began his experience in this field when he completed an undergraduate honors thesis in biology at Harvard on physique and reflexes of the autonomic nervous system. At that time, Hunt rated photographs of a group of Harvard undergraduates by Sheldon's longer, photogrammetric procedure which today is in disuse (Hunt, '42).

Before 1940, when Sheldon and his earliest students were the only somatotypers, this group showed close agreement in their photographic assessments. For example, Sheldon and Tucker rated a series of 200 young men and obtained a correlation of +0.95 for the 600 evaluations of the three components, considered as a single aggregate (Sheldon, Stevens and Tucker, '40).

From 1946 to 1954, Hooton and his associates diverged considerably from Sheldon's original formulations and methods of rating. These divergences grew from the experience of the Harvard group in evaluating photographs of over 40,000 men in the U. S. Army. These workers renamed their method "body typing," and the three components "fat," "muscularity," and "attenuation." Fat and muscularity were rated by inspection of photographs. Attenuation was measured by means of a 7-point scale of equal intervals of the inverse ponderal index (stature/$\sqrt[3]{\text{weight}}$).

In 1947, Hunt completed a course in body typing at Harvard under Hooton, but was never active enough in the Army program to adopt fully Hooton's revised standards of rating.

From the two divergent schools of investigators have come two standard photographic atlases for White adult mal that of Hooton ('51), and the work Sheldon, Dupertuis and McDermott ('5 For younger adolescent or prepubesc boys, however, no such atlas is availa from either school. At such ages, simplest alternative is to arrange pho graphs in rank order according to th degree of manifestation of one compon at a time.

Rank-ordering actually antedates Sh don's adoption of the 7-point scale of pression of the three components. Bef defining these scales in at least partia morphological terms, Sheldon had ra ordered thousands of body build pho graphs (Sheldon, Stevens and Tucker, '4

As part of an experiment on compone ratings and factor scores, Howells ('5 asked Hunt to rank-order 30 young Ar men in the first component on two casions, separated by an interval of t years. Hunt's agreement with himself (liability), as indicated by Spearman's ran order coefficient of correlation, w +0.958. For mature males, then, Hun ratings seem fairly stable.

Accordingly, in the present work adolescent boys, Hunt visually rated t prepuberal photographs in the first a second components. Each prelimina ranking of a single component was p formed in one day, and a few final a justments made on a later day. So weeks later, the same procedure was a plied to the subadult photographs of the boys. At both ages, the third compone was measured by Hooton's method, b without his 7-point scale intervals. I stead, Hunt directly calculated the inver ponderal index of stature in centimete divided by the cube root of weight in ki grams.

In these adolescent photographs, the bows are usually relaxed, so that the upp extremity is not in the rigid pose whi most raters prefer to use in assessing th region. Hunt therefore minimized it in h ratings of the whole body.

When the ordinal ranks of all 71 bo had been determined at both ages, the ranks were compared by means of Spea man's rank-order coefficient of correlatio The inverse ponderal indices at the tw

were correlated by means of the prod- noment coefficient.

'indings on the adolescent sample

ıe basic correlations for the three com- nts are as follows:

Component	r
1	+0.453
2	+0.501
3	+0.708

ridently the visual first and second ponents are far less predictable ıgh adolescence than is the metrical component. This index is close to value found by Deming ('57) in cor- ing prepuberal and mature recumbent hs of 24 boys: namely, +0.736.

the two ages in our data, the means standard deviations of the index are:

	Mean	S.D.
Prepuberal	43.9	1.5
Subadult	44.2	1.3

ıe prepuberal values of the index are ficantly and negatively correlated with later changes in adolescence ($r = $ '3; $p < .001$). If x represents the uberal index, and y the subadult value, east squares regression of y on x is:

$$y = 18.3 + 0.6x \; (S.E._{est} = 0.9).$$

ın be shown from this equation that nuated" boys with high values of the x at 11.5 years of age tend to become so in their later teens: while stocky tend to become more attenuated.

ıe correlations for the two visual com- ents are so low that we may even der whether the pre-existing physique bliterated" during adolescence. Alter- vely, however, errors or idiosyncrasies unt's ratings may be great enough so an uncorrupted assessment of the ponents might yield higher coefficients. possible to explore this problem by paring Hunt's evaluations with those ther experienced workers.

upertuis and Emanuel ('56) have vn that divergences among raters may ppreciable. Their study was based on ıgs of photographs of 500 Air Force ıg personnel. Dupertuis rated the pho- aphs by Sheldon's inspectional or "an- poscopic" method, and Hooton and . Stagg by their system of body typing. The correlations between the two methods were:

Component	r
1	+0.82
2	+0.83
3	+0.86

Still more relevant to Hunt's own ratings is a set of correlations between a number of observers, including Hunt. These workers evaluated a set of 28 to 30 photographs of White men in the U. S. Army, selected for representativeness of physique on the basis of frequencies of Hooton's body types in over 39,000 men who were photographed during their separation from the service after World War II. Howells ('57) identifies the raters as follows: *Lab* is a rating by a team trained, supervised and reviewed by Hooton. *A* is one of Hooton's chief associates, who rated the small Army sample by himself some years later. *X* is an adherent of the Sheldon method who is currently active in physiology. *Y* is one of Sheldon's major collaborators. The ratings of *X* were done by inspection only: while *Y* applied Sheldon's entire anthroposcopic technique, including considerations of age, stature and weight. All workers used the 7-point scale, including intermediate values such as 3.5 whenever necessary, and evaluated only the first and second components.

The correlations between these raters are presented to the right of the asterisks in table 1. Agreement is usually closer in the first component than in the second, unlike the finding of Dupertuis and Emanuel ('56). We shall now review the basic correlations in table 1 by means of factor analysis.

Consensus and idiosyncrasy among body typers: a problem in cultural conformity and deviance

Since all of the preceding 5 raters shared at least some cues from the photographic images as a basis of their judgments, their intercorrelations can be subjected to a simple factor analysis. We may thereby distinguish between a major factor of common cultural tradition in rating, and residual measures of deviance. From a somewhat different point of view, Thurstone and Degan ('51) once applied a

factor analysis to the decisions of justices of the U. S. Supreme Court.

In the present case, the factorial procedure is based on the work of Spearman, as expounded particularly in Spearman ('27) and in Spearman and Wynn Jones ('50). The plan of computation is especially well described in Thomson ('51).

For decades, many psychologists have administered batteries of standardized tests to groups of experimental subjects. When the scores from these tests are organized into a matrix of intercorrelations, quite often all the tests share appreciable loadings of a general factor. Spearman called it "g," and assumed it to be a basic intellectual characteristic analogous with "mental energy." Many other factorial methods are now in use, and in some of these routines, "g" is simply the "first factor" in a more extended program of computations (Thomson, '51).

In using Spearman's procedure, one first measures the g loading of each of the original tests. Each original correlation in the matrix contains some g from each of its two constituent tests. One then removes this g from the coefficient, leaving a smaller residual correlation. The residuals are then combined into a new matrix. If all the coefficients in the residual matrix are only insignificantly divergent from zero, one may conclude that the original matrix had a large saturation of g, and perhaps each test then has only inconsequential amounts of residual variation. If the investigator is interested only in g, he may thereafter use only the most g-saturated tests in the original battery.

This method may sometimes be useful in physical anthropology. For example, if many of the existing methods of measuring hydration and fatness have been concurrently applied to a group of test subjects, one may thereafter rely on the most g-saturated few measures for future investigations. The present study of physique, again, represents multiple estimates of certain scales of somatic variation. Since we are dealing with many raters, it seems useful to define g as "consensus." Each rater is now the analog of a single psychological test, and we can measure his "consensus loading." A rater with a high loading is a "conformist," and one with a lesser amount of consensus is a "devia
From all these loadings, we compute
residual correlations between raters.
table 1, the consensus loadings of
raters are in a column at the extreme ri
and the residuals are located to the
of the diagonal asterisks.

Findings on consensus

In the first component, Hunt and
server *X* have the highest consensus l
ings: whereas *Lab* and *Y* are the devia
In the second component, considerable
versal of the loadings occurs, with H
and *X* as the deviants. Disagreem
among raters in most cases is greater
the second component than for the fi

Of all the raters, Hunt and *X* share
most experience in measuring the
cutaneous adipose layer from skinfolds
radiographs. This background may h
led both men to equate the first comp
ent rather efficiently with subcutane
adiposity. The present authors feel,
fact, that this equivalence should be c
sciously cultivated. Perhaps the low c
sensus loadings of Hunt and *X* in the
ond component reflect their skeptic
concerning the anatomical rationale
this scale of somatic variation—again
cause of experience with radiograp
measurements of inner tissue shadows

For a sample of 28 to 30 cases,
magnitude of a residual to be significan
divergent from zero would have to exc
±0.35. None of the residuals in tabl
even approaches this size. From this
dence alone, one might conclude that
simple polarity exists between the scho
of Hooton and Sheldon, and each ra
seems to be on his own.

Despite this evidence of idiosyncra
these workers have not yet arrived at
"tower of Babel" stage. Furthermo
Howells ('57) has undertaken a very
tensive factor analysis of the anthro
metric measurements and ratings of p
sique in this same Army sample, a
found fairly clear-cut differences betw
the ratings by Hooton's students (*Lab*
and Hunt), and those by Sheldonians
and *Y*. In the first component, the H
vard group somewhat emphasized sho
ness and bulk of the whole trunk, a
some reduction of limb lengths. T

TABLE 1

Correlations, consensus and residuals in five ratings of physique in 28–30 men in the U. S. Army

	Hunt	Lab	A	X	Y	Consensus loading
			First component			
Hunt	*	+ 0.87	+ 0.87	+ 0.89	+ 0.84	0.974
Lab	+ 0.04	*	+ 0.87	+ 0.79	+ 0.66	0.869
A	– 0.02	+ 0.07	*	+ 0.83	+ 0.75	0.917
X	– 0.02	– 0.02	– 0.03	*	+ 0.86	0.935
Y	+ 0.02	– 0.07	– 0.02	+ 0.07	*	0.840
			Second component			
Hunt	*	+ 0.70	+ 0.67	+ 0.66	+ 0.81	0.821
Lab	0.00	*	+ 0.80	+ 0.69	+ 0.73	0.852
A	– 0.05	+ 0.05	*	+ 0.82	+ 0.70	0.879
X	– 0.04	– 0.03	+ 0.08	*	+ 0.74	0.849
Y	+ 0.09	– 0.02	– 0.07	0.00	*	0.875

d is toward squatness rather than eu-
ıoidism. The Sheldonians, however, e clearly stressed bulk of the waist and h, and taper (but not shortening) of limbs. As Howells cogently puts it, Sheldonians think of an extreme en-orph as a "gutball." These subtleties d not have been revealed through com-ıtions as crude as Spearman's factor ysis of the ratings alone.

Continuity and error in adolescent physique

he concept of consensus is now to be ied to Hunt's assessments of compon- 1 and 2 in the adolescent sample. test is based on two assumptions: , that consensus is the basic scale of atic variation for each component se predictability we wish to reveal ı Hunt's adolescent ratings. The sec- assumption is that Hunt's loadings of sensus in rank-ordering immature boys equivalent to those based on his use 7-point scales on grown men. Our istical test is the hypothesis that the lictability of consensus for compon- 1 and 2 through adolescence is not ificantly different from that of the rse ponderal index.

or our symbolism, we let c = consen- loading, subscripts 1 and 2 represent ponents 1 and 2, and subscript 3 esent the index.

y the preceding hypothesis, the ex-ed correlation between the prepuberal subadult ratings of components 1 or 2 should be given by the product of the appropriate c value and our observed correlation for the index:

Component	Expected correlation
1	$r_1 = c_1r_3 = 0.974 \times 0.708 = 0.689$
2	$r_2 = c_2r_3 = 0.821 \times 0.708 = 0.581$

For components 1 and 2, the preceding expected correlations are converted into z scores, and the significance of their divergences from the "obtained" correlations is evaluated by the t test, where the sample size of 71 boys is the basis of our standard error of z (Snedecor, '56). We find that the following values occur:

Component	t	p
1	2.95	<0.01
2	0.93	>0.05

From these findings, it seems that however we may "purify" the rating of the first component by a consensus of experienced workers, it is still not as predictable during adolescence as is the inverse ponderal index. Consensus on the second component, however, is only insignificantly less predictable than one might expect from the index.

DISCUSSION

Considerations of body composition and growth may help us to interpret these findings. The inverse ponderal index, after all, is based on stature and weight. During adolescence, stature usually increases to almost the individual's lifelong maximum. According to Davenport ('44), the only minor exception to this increase is

the occasional transient shortening of long bones at puberty—especially in girls.

Weight is the other measurement in the index. It is mainly non-adipose, and its lean fractions for the most part either grow or stabilize in adolescence. The major exception is lymphoid tissue, which shrinks (Scammon, '30). The adipose portion of body weight, however, may increase, stabilize or shrink in adolescence, depending on the caloric balance of the individual. It would appear that adolescence in boys is often a caloric "revolution," whose intensity cannot efficiently be forecast from a nude photograph at 11 1/2 years.

The second component, on the other hand, is a very crude perception of deeper tissues which *do* enlarge in adolescence. In the absence of rating error, theoretically it appears to be virtually as predictable as the index. This error seems to characterize all 5 raters in our study of adult males, however, so that in practice we may doubt whether one person could attain this level of accuracy in his predictions.

Moreover, even "purified" or highly conformist predictions of the second component seem to give small comfort to Sheldon and his followers, who have long hoped to reveal a regular and predictable life cycle for each somatotype (Sheldon, Dupertuis and McDermott, '54), and to combine the two patterns into an expression of genetic endowment called the "morphogenotype." Instead, our evidence seems to support Hooton's conservative opinion on body typing; that ratings are transient estimates of physique. In other words, a rather broad range of alternative patterns of development may lead to outwardly similar mature individuals.

Under such circumstances, it may be unwise to relate the three components to embryonic germ layers, as Sheldon, Stevens and Tucker ('40) have done, or even to later developmental stages, as the senior author has alternatively suggested (Hunt, '49, '52). Instead, tissue size seems to be the simplest rationale of any theory of "components" of physique.

In such terms, the first component seems to be more defensible than the second. As Edwards ('50), Reynolds ('51), Br and Keys ('51), Garn ('54), Hamm ('55), Lindegård ('56) and others h shown, adipose thicknesses at diffe subcutaneous sites show considerable variation or communality, so that a son tends to be more or less lean or pose all over.

The subcutaneous layer contains s but not all of the extractable fat in body, and measurements and ratings its thickness certainly do not directly dicate how much inner fat lies near viscera, muscle fibers, or nerve c Nevertheless, in young adults at least, subcutaneous and inner adipose depo are balanced well enough so that su ficial estimates of adiposity agree fa satisfactorily with calculations of t body fat from underwater weighing (pertuis et al., '51; Brožek and Keys, '52). In the young, then, Hooton's component is an apt and realistic conc

During aging, inner fat often accu lates more rapidly than does fat in subcutaneous layer (Brožek, '52; Šk Brožek and Hunt, '53). The composit and elasticity of the skin and subcutane layer change, and sizeable individual ferences occur in the sites and amou of accumulated inner adipose tissue (ner, Mazzoleni and Rodriguez, '55). Th age changes detract from the predicta ity of total body fat from skinfolds (žek and Keys, '51), and somewhat und mine the concept of adiposity as an o all "component" of the elderly organi

In measuring fatness in man, we m now ask whether photographic ratings the first component are preferable to sessments of the subcutaneous layer fr skinfolds or radiographs. In general, basic correlations between raters of t component in table 1 are lower than th between different measurers using sk fold calipers. Even with the old Fran caliper, with unspecified pressure and a of contract, Meredith ('36) found co lations between different anthropometr of +0.940 and +0.948 in measureme of skinfolds in children. With this calip Hammond ('55) found that repea measurements by one person were in o slightly better agreement than those different investigators. He also found t

ment is somewhat improved by the f the newer Harpenden caliper, with lardized pressure and area of contact the skinfold. Using another type of lardized caliper, Newman and White d correlations between partly-trained surers at 4 skinfold sites which ranged +0.916 to +0.955 (Keys and Bro- '53).

successive standardized radiographs, surements of tissue shadows are at as reliable as skinfolds, and in some s are more so (Clarke, Gëser and sdon, '56; Baker, Hunt and Sen, '58). here living persons can be measured, tandardized x-ray films taken, we efore prefer skinfolds or measure- ts of adipose tissue shadows to ratings ne first component, for reasons of ob- vity, modesty and simplicity.

ıeldon, Stevens and Tucker ('40) con- red the original second component somorphy) to be a concurrent esti- e of muscle size and bone size. From rnal photographs of the body, such nates are apparently inaccurate. For nple, Harper ('54) found that "ap- nt" muscle size as rated from photo- hs is virtually uncorrelated with the al sizes of muscle shadows as meas- from radiographs. Furthermore, the s of muscles and bones in the limbs nearly independent of each other ynolds, '44; Baker, Hunt and Sen, '58). cle sizes in different regions of the , however, do show some covariation n measured from x-ray films, and in sense we may still speak of a com- ent of muscularity (Baker, '58, per- l communication).

till another difficulty with the second ponent is that no factor akin to it has been revealed through factor analysis external body measurements. Some- t better analogies have been demon- ted between factors and concepts such he first component or caloric nutriture nner, '47; Howells, '52, '57; Lasker, Hammond, '57).

Ve are left, then, with a second com- ent which expresses muscle relief, seness of skin and features, masculin- and strength. It can be seen in the ng or in suitable photographs, but can- yet be measured in either. Further- more, different observers no longer agree closely on how to rate it.

In view of these difficulties, most future research which bears on muscularity should probably be based on direct measurements rather than on photographic ratings. Often, these measurements may be designed to show "parsimoniously" the effects of local mechanisms of growth (Baker, Hunt and Sen, '58; Hunt, '58). At least in radiographs of the brachium, some improvement of reliability in measuring muscle shadows can be attained when the muscles are contracted rather than relaxed (Clarke, Gëser and Hunsdon, '56).

Although Sheldon's concept of the constancy of physique certainly does not hold during adolescence, we suggest that it still has some validity over the younger years of adulthood. As Finlay ('57) has observed, the non-adipose constituents of the mature body show enough metrical continuity so that one may speak of them as rather stable, "constitutional" characteristics of the individual. The evidence indicates, however, that body build photographs do not permit us to make precise statements on this stability: whereas such statements may be somewhat more credible when the "inner man" beneath the subcutaneous layer is measured.

SUMMARY

Stolz and Stolz ('51) have described the somatic changes in a series of adolescent boys who were remeasured for several years in Oakland, California. We have used serial body build photographs of this series for a study of physique and sexual maturation in adolescence. On 71 boys, the photograph nearest the age of 11.5 years was defined as the "prepuberal" age level, and an older photograph taken between 16.5 and 19.0 years was assumed to be at the "subadult" stage of development.

The senior author (Hunt) rank-ordered the prepuberal and subadult photographs according to the first and second components of physique, and calculated the third component as equivalent to the inverse ponderal index (stature/$\sqrt[3]{\text{weight}}$). The correlations between the ratings are based on the rank-order formula, and between values of the index by the product-

moment coefficient. Agreement at the two ages was worse for the first component, slightly better for the second, and by far the best for the index. The adolescent change in the index was found to be negatively correlated with the index at the prepubescent age.

Since experienced workers show only limited agreement today in their ratings of body build photographs, the hypothesis was tested that the first and second components are really as predictable as the index through adolescence, but that the lower observed correlations were produced chiefly by Hunt's idiosyncrasies of rating. This test was made through a factor analysis of agreement of his ratings with 4 others made on a set of photographs of men in the U. S. Army.

This test showed that the correlation of the second component could be explained by this hypothesis, since it (like the index) is based mainly on tissues which continue to grow in adolescence. The first component, however, is related to adipose tissue. In adolescence, some boys fatten, others stabilize, and still others thin down. It would appear that the alternative of adipose shrinkage tends to depress the predictability of fatness from early to late adolescence. In fact, radical changes are sometimes seen. Consequently, similar physiques in the adult may be attained by quite different developmental paths in different individuals.

These findings add to the theoretical and practical difficulties of rating physique from photographs. Observers generally do not agree as well in assessing the first component as do workers who measure the subcutaneous layer from skinfolds or radiographs. The second component is a score related in part to the bulging of muscles, but it is not appreciably related to muscle size. Observers today agree less well on rating it than they do on the first component. Furthermore, the sizes of muscles and bone are not highly correlated with each other. Factor analyses of body measurements, too, have failed to reveal a factor resembling the second component. For most purposes, therefore, direct measures of inner tissues seem preferable to photographic ratings of the second component.

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Dr. S. S. Stevens very generously [...] mitted us to study the present serie[...] adolescent photographs. The raw data [...] our study of adult males came f[...] Howells ('57). Drs. A. Damon, J. Gallagher, F. P. Heald, C. F. A. Moor[...] and W. W. Howells offered especially v[...] able advice.

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e Weight of the Dry Fat-free Skeleton of American ites and Negroes[1]

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ie characteristics of bone are the total
ession of extrinsic and intrinsic fac-
acting upon it. Thus, weight, one of
characteristics, is influenced by these
rs. Ingalls ('31) stated: "Develop-
of bone is never completed, but the
itions presented at any given moment
he end results of a certain hereditary
lex interacting with some particular
ronment for a given length of time."
iat the same bone of different in-
uals, or that different bones of the
individual, are affected to the same
ee by these complex factors is not to
xpected. Bauer, Aub, and Albright
) demonstrated that bone trabeculae
titute the main storehouse of calcium
that a measurable reduction in trabec-
occurs in animals placed on a low
um diet. Ingalls ('31) found the ster-
and sacrum—both largely cancellous
s—to be the most variable in weight
e bones of 100 White male skeletons.
ndicated further that differences in
ht occur in each region of the verte-
columns of these skeletons with a
ressive increase in the coefficients of
ition extending from the skull cau-
, i.e., the cervical vertebrae, with rela-
y more compact bone than the other
ients, are less variable in weight from
mn to column than are the lumbar
ebrae and sacrum, which have rela-
y more cancellous bone.
sing radioactive strontium, Pecher
) measured the activity of "shaft and
ecular bone" in recently injected rats
rabbits, and found trabecular bone
ave a higher activity than shaft bone,
that "activity was higher in the dorsal
ebrae than in most of the other bones."
esy ('45) attributed the difference in
rate of renewal of epiphyseal and diaphyseal bone to the richer circulation of epiphyses. He demonstrated with labelled phosphate that during the course of 50 days 29.7% of inorganic phosphate in an epiphysis of the femur was renewed, whereas only 6.7% of inorganic phosphate was renewed in the diaphysis of the same bone. A similar relation was seen between epiphysis and diaphysis of the tibia. However, the ribs and scapula had an average renewal of 27.5% and 43.8%, respectively.

Age is definitely expressed in bones (Todd, '27), and that the weight of bones is altered by aging has been presented by Ingalls ('31). In his study of 100 White male skeletons ranging in age from 19 to 78 years, the material was grouped in 5 ten-year age periods. The skeletons were from the Todd Collection and had been prepared by routine maceration, cleaning, and air-drying, but were not degreased. He recognized that the preparation had not resulted in the same condition for all of the bones, but he was interested in relative rather than absolute values. He found that the maximum physiological development of the skeleton occurred "somewhere around 35 years of age." Following this peak, there was a decline in bone weight to age 45 years. Beyond this age, the weight again increased reaching the highest value for the series in the sixth decade; however, this increase was interpreted to be the result of aging or pathological processes forming new bone around the articular surfaces and upon the skull. From age 55 years, the weight again decreased, reaching its lowest value "between 65 and 70 years."

The weights of the skeleton and of selected bones have been utilized in deriving

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formulae for estimation of skeletal weight in the living (Trotter, '54; Merz, Trotter and Peterson, '56). It was found by Baker and Newman ('57) that broad categories of living weight can be predicted from skeletal weight and that the correlation between weights of individual bones or of subdivisions of the skeleton may be helpful in the segregation of commingled skeletal remains. The usefulness of weights of long limb bones in the determination of their sex has been presented by Vallois ('57).

Lowrance and Latimer ('57) studied a series of skeletons of Asiatic origin of unknown age and sex. They presented the mean percentage contributions to the total skeleton weight by individual bones.

A survey of the content of strontium-90 in man (Kulp, Eckelmann, and Schulert, '57; Eckelmann, Kulp, and Schulert, '58) has indicated a need for absolute values of the weight relationship of given bones and groups of bones to the total skeleton weight. Single bones, usually a rib, vertebra, or femur shaft, were analyzed for content of strontium-90, and from these small samples an estimate of the amount of strontium-90 in the total skeleton was determined on the basis of the relation of the weight of the sample to the weight of the total skeleton. In their report ('57) the final values for the world-wide human assay were "normalized" by using unpublished data based on weights of a few skeletons in this laboratory. Although the authors have maintained the analytical error to the lowest possible value, the "errors on the individual measurement range from 2 to 50 per cent" with "most of the samples having an error of the order of 5 to 10 per cent." They propose that the analytical error is quite small compared with the degree of uncertainty of the relation between the amount of strontium-90 assimulated by an individual bone and that by the whole skeleton. Thus, they recognized that different bones of the skeleton as well as different parts of the same bone are in varying states of metabolism at any one time. It should be recognized, also, that the weight relationships of parts of the skeleton to the whole may vary among groups and that failure to take this into account in a world-wide survey will result in further error in estimates of stro tium-90 content in the total skeleton.

The purpose of the present undertaki is a comparative study of the weight the total skeleton and the contributions it by 4 arbitrary divisions and by individu femurs based on skeletons of Americ Whites and Negroes.

MATERIAL

A series of 100 dry, fat-free skeleto evenly divided among American Whi and Negroes of both sexes and showing gross pathology, were chosen. The me ods of preservation of the cadavers bef skeletonization are summarized as follow

Unembalmed	Embalmed			
Frozen[1]	GAC[2]	GAC + F[3]	F[4]	Unkn
	White male			
22	1		2	
	White female			
12	4	4	4	
	Negro male			
18	3		2	
	Negro female			
7	12	2	2	

[1] Cadavers are retained in the morgue of medical school for a minimum of 30 days a temperature of −15° to −20°C.
[2] Solution of glycerin (two parts), 95% alco (two parts) and dissolved carbolic acid crys (one part).
[3] 3% formalin.
[4] 10% formalin.

The majority of the bodies were une balmed, and had had a complete or par autopsy before delivery to this departme For the autopsy the usual procedure of moving the anterior chest wall by a tra verse cut through the manubrium ste and longitudinal cuts on either s through the ribs had been followed. T only other cuts affecting the skeleton w through the calvaria when the post-m tem examination involved the head. an earlier study in this laboratory, Tro and Peterson ('55) found that the st of the cadaver, either embalmed or une balmed, does not affect the weight of ash of the bones in percentage of their c fat-free weight and concluded that the c fat-free weight of a bone is not altered embalming.

TABLE 1

Age distribution of skeletons according to race and sex

ace	Sex	Age interval (years)						Total
		25–39	40–49	50–59	60–69	70–79	80–100	
hite	male	0	1	5	8	11	0	25
hite	female	1	3	4	5	7	5	25
egro	male	1	5	5	6	7	1	25
egro	female	4	4	3	3	6	5	25
otal		6	13	17	22	31	11	100

e age distribution of the 4 groups ac- ng to race and sex is presented in 1. The White male and female s range in age from 25 to 91 years, with a mean age of 66 years. The male and female groups range from 100 years with a mean age of 60 and ars, respectively.

METHOD

er removal of the soft parts, the skel- were prepared by the Terry Method y, '32) excepting the last step, that mersing the bones in a thin solution e. Rather, after they had been sub- l to benzol vapors, they were im- ed in acetone, dried, and weighed ter and Peterson, '55).

ights of the bones were determined a Toledo beam balance. The bones weighed individually with the excep- of the bones of the cranium,[2] hand, ribs and moveable vertebrae. The ribs weighed as right and left groups; the able vertebrae were weighed in ac- nce with their topographical location vical, thoracic, and lumbar. No at- t was made to weigh the coccyx,[3] os- of the ear,[4] or the hyoid bone. The of the individual weights of a given ton is considered to be the total skele- eight.

determining the weight of the skull, rrection was made for missing teeth he corresponding alveolar borders. It ognized that some error is introduced e absence of teeth, whether they were re- or post-mortem. The distribution eletons (in per cent) according to er of teeth in each jaw is summar- for each racial group as follows:

	0 teeth	1–8 teeth	9–16 teeth
	White		
Maxillary	34	8	8
Mandibular	28	13	9
	Negro		
Maxillary	9	21	20
Mandibular	8	19	23

The dry, fat-free weight of one complete set of permanent teeth in a White male, age 50 years, was found to be 39.0 gm. The weight of the maxillary teeth, 19 gm, was approximately the same as of the mandibular teeth, 20 gm. The total teeth were found to contribute 5.5% of the skull weight, 712 gm. In this series of skeletons only two Negro female skeletons presented a complete set of teeth, and in 43% there were no maxillary teeth and in 36% no mandibular teeth.

Each skeleton was divided into 4 arbitrary divisions: I, skull; II, vertebral column, ribs and sternum; III, superior extremities; and IV, inferior extremities. In addition, the femur weights were used in comparing a single bone weight to the total skeleton weight.

In the statistical treatment, the 4 groups of skeletons were compared by the analysis of variance to determine whether there are significant race or sex differences among total skeleton weights, among each of the 4 division weights, among the weights of the femurs, and among the percentage contributions of each division and of femurs to total skeleton weight. In addition,

[2] *Cranium* is used to designate skull without mandible.

[3] Except when the whole or part of it was fused to sacrum; it was then included in the weight of sacrum.

[4] Except when retained in the temporal bone after maceration.

the analysis of covariance, correcting for differences among total skeleton weights was used to compare weights of the 4 divisions and of the femurs (Snedecor, '57). Grateful acknowledgment is made to Barbara Bartels Hixon for selection of the statistical methods and for guidance in accomplishing the analyses.

RESULTS

Total skeleton weight

In table 2 are presented the means of the total skeleton weights according to race and sex. The mean total skeleton weight of White males, 3418.7 gm, is greater than of White females, 2302.5 gm; and of Negro males, 3852.7 gm, than of Negro females, 2828.2 gm. The two groups of Negro skeletons have a mean weight of 3340.2 gm and are heavier than the two groups of White skeletons with a mean weight of 2869.6 gm; the two groups of the male skeletons, mean weight of 3635.7 gm, are heavier than the two groups of female skeletons, mean weight of 2565.4 gm. The differences among the 4 groups are presented graphically in figure 1.

An analysis of variance of the mean total skeleton weights of the 4 groups was carried out as shown below.

Highly significant differences ($P < 0.001$) are found among the mean skeleton weights of the 4 groups. A breakdown of the source of variation into race, sex, and interaction of the two shows the Negro skeletons to be significantly heavier ($P < 0.001$) than the White, and the male skeletons to be significantly heavier ($P < 0.001$) than the female, with no significant interaction.

Division I, skull

The mean weights of the skull, are presented according to race and sex in table 2 and figure 2. In the White groups, the mean weight is greater in the male, 632.9 gm, than in the female, 498.9 gm; h ever, in the Negro groups, the differe between the mean weights of the s of the two sexes is slight, 668.1 gm males and 643.2 gm for females.

Using the analysis of variance as ab it is found that there are significant ferences ($P < 0.001$) among the s weights of the 4 groups. A breakdow the three degrees of freedom among 4 groups shows the interaction of race sex to be significant ($P < 0.05$) indica an irregular pattern of the mean weigh the skull between the sexes within e race.

Because the interaction is significant mean square for "Within groups" is longer the appropriate error term to for testing race and sex differences. mean squares for these two source variation are not significantly larger t for the interaction. Therefore, no defi conclusion can be reached from this an sis concerning sex or race difference

To test the possibility that differe in the mean total skeleton weights of 4 groups may be obscuring differe among the mean skull weights of th groups, an analysis of covariance in w the effect of differences in total skel weights is removed was applied.

Significant interaction ($P < 0.05$ still present, and the mean squares Negro vs. White and for Male vs. Fe are smaller than for the interac Therefore, no significant difference skull weights between the races or s have been found in these data.

The mean per cent contributed by skull to total skeleton weight of eac the 4 groups is presented in table 2 figure 3. The percentage contribu ranges from 17.5% in the Negro r series to 23.0% in the Negro female se It is greater in the female series of races (22.5%) than in the male serie

Source of variation	Degrees of freedom	Mean square	Variance ratio (F)	P
Among 4 groups	3	11,483,304	41.2	<0.00
Negro vs. White	1	5,756,639	20.7	<0.00
Male vs. female	1	28,640,692	102.8	<0.00
Interaction	1	52,581		n.s.
Within groups	96	278,609	1	

TABLE 2

eans and standard deviations (S.D.) of the total skeleton weight and the weight and the contribution of each division in per cent of total weight according to race and sex

Division	Weight in grams		Per cent of total skeleton weight	
	Mean	S.D.	Mean	S.D.
	White male			
otal skeleton	3418.7	496.3		
I, Skull	632.9	137.5	18.5	3.20
II, Vertebral column, ribs and sternum	582.2	123.4	16.9	1.83
III, Superior limbs	634.3	107.8	18.5	1.20
IV, Inferior limbs	1569.2	253.0	46.0	3.16
	White female			
otal skeleton	2302.5	482.3		
I, Skull	498.9	97.2	22.0	3.85
II, Vertebral column, ribs and sternum	408.6	104.1	17.7	2.08
III, Superior limbs	374.8	91.0	16.2	1.27
IV, Inferior limbs	1020.1	253.7	44.0	3.25
	Negro male			
otal skeleton	3852.7	540.2		
I, Skull	668.1	101.1	17.5	2.68
II, Vertebral column, ribs and sternum	669.4	124.6	17.3	1.43
III, Superior limbs	751.2	105.2	19.5	1.02
IV, Inferior limbs	1764.2	300.0	45.6	2.67
	Negro female			
otal skeleton	2828.2	586.8		
I, Skull	643.2	145.3	23.0	3.79
II, Vertebral column, ribs and sternum	507.8	124.2	17.9	1.89
III, Superior limbs	476.8	102.0	16.8	0.69
IV, Inferior limbs	1200.3	303.3	42.2	3.93

races (18.0%). In the two racial ps the per cent of total skeleton weight ributed by Division I is the same 25%).

the analysis of variance the mean entage contributions of the skulls to skeleton weights of the 4 groups are d to be significantly greater ($P <$ 1) in the female groups than in the . The differences between the races the interaction of race and sex are significant.

Division II, vertebral column, ribs and sternum

he mean weight of division II (table 2; e 2) is heavier in White males, 582.2 than in White females, 408.6 gm; and egro males, 669.4 gm, than in Negro ales, 507.8 gm.

y the analysis of variance, the race and differences are found to be highly significant ($P < 0.001$). However, by the analysis of covariance, in which adjustment is made for differences among the mean total skeleton weights of the 4 groups, division II is found to be significantly heavier ($P < 0.001$) in the males than in the females with no significant difference between the races nor with significant interaction of race and sex.

The mean per cents contributed by the vertebral column, ribs, and sternum to total skeleton weight of each of the 4 groups are presented in table 2 and figure 3. The contribution by this division is essentially the same in the Negro group (17.0%) as in the White group (17.3%). Although the difference between the sexes, female, 17.8% and male, 17.1% , is slightly larger but not significantly so, it should be noted that the variance ratio (F) of 3.62 approaches the minimum probability level used in this study. It is possible that

a larger sample might show a significant sex difference.

Division III, superior limbs

The mean weights of the skeleton of the superior limbs of the 4 groups are presented in table 2 and figure 2. In the White group, the mean weight is greater in males, 634.2 gm, than in females, 374.8 gm; in the Negroes, the mean weight is also greater in males 751.2 gm, than in females, 476.8 gm.

Before adjusting for the differences in the mean total skeleton weights of the 4 groups, highly significant differences ($P < 0.001$) were found.

After adjustment for the differences in the mean total skeleton weights of the 4 groups was made using the analysis of covariance, a significant difference ($P < 0.001$) persists. A breakdown of the three degrees of freedom among the 4 groups shows that the skeleton of the superior limbs of the males is significantly heavier ($P < 0.001$) than of the females, and of the Negroes ($P < 0.01$) than of the Whites, with no significant interaction.

The mean per cents contributed by t[he] skeleton of superior limbs to total skel[eton] weight of each of the 4 groups are sh[own] in table 2 and figure 3. In the W[hite]

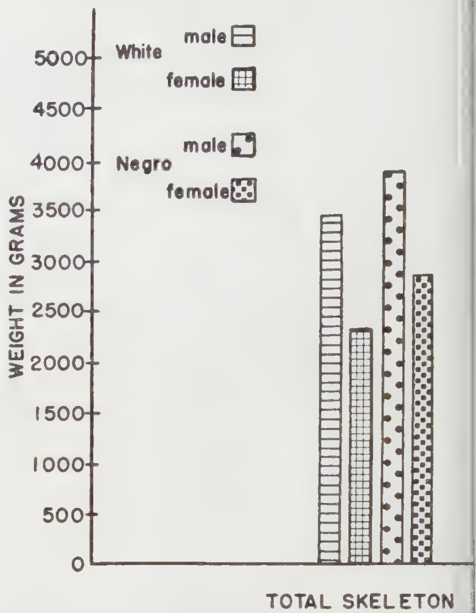

Fig. 1 Block graph of total skeleton w[eight] according to race and sex.

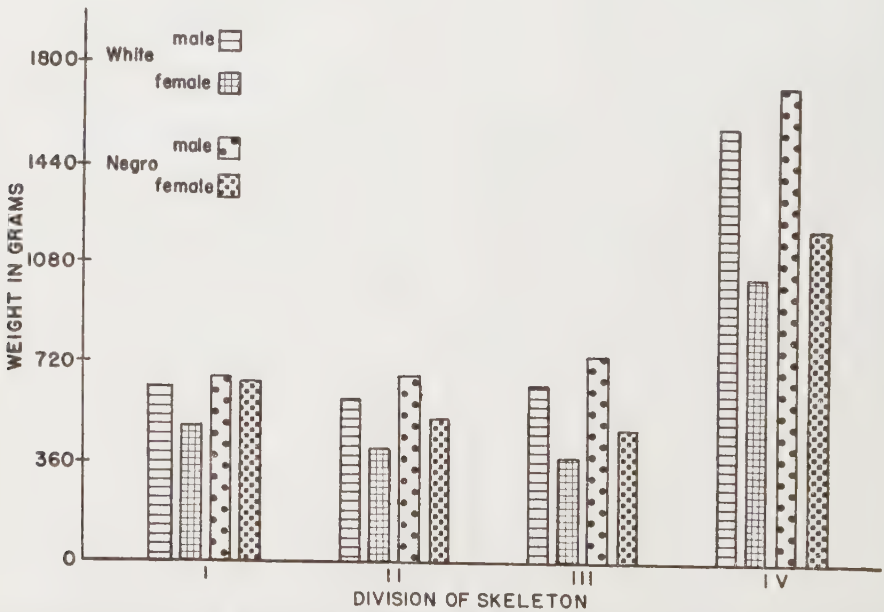

Fig. 2 Block graph of the absolute weights of skull (division I); vertebral column, ribs and sternum (division II); skeleton of superior limbs, (division III); and skeleton of inferior limbs (division IV) according to race and sex.

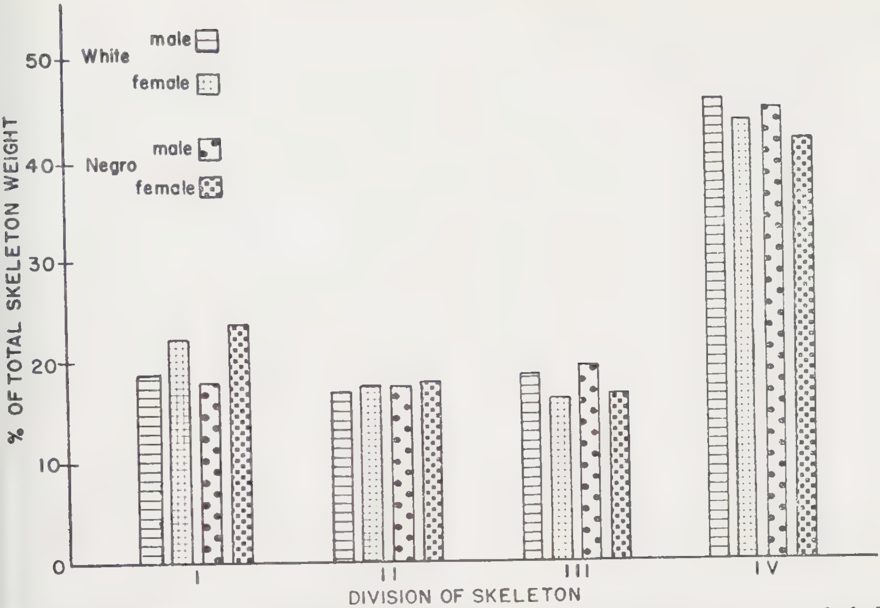

Fig. 3 Block graph of the percentage contributions to total skeleton weight of skull (di-ion I); vertebral column, ribs and sternum (division II); skeleton of superior limbs (di-ion III); and skeleton of inferior limbs (division IV); according to race and sex.

the superior limbs of the male con- a greater amount (18.5%) to the keleton than of the female (16.2%). groes, the same pattern is evident, ale contributing 19.5% as compared 16.8% of the female. The per-;e is greater (18.2%) in the Negroes n the Whites (17.4%).

ng the analysis of variance, race and fferences are found to be highly sig-nt ($P < 0.001$), with the superior of the Negro group contributing a cantly greater ($P < 0.001$) percent- the total skeleton weight than of the group, and the superior limbs of ales contributing significantly more 0.001) to the total skeleton weight of the females. No significant inter- is present.

Division IV, inferior limbs

mean weight of the skeleton of the or limbs (table 2; fig. 2) is heavier in males, 1569.2 gm, than in White es, 1020.1 gm; and in Negro males, 2 gm, than in Negro females, 1200.3

ore adjustment for the differences g the mean total skeleton weights of the 4 groups, the race and sex differences appear to be highly significant ($P < 0.001$), with no significant interaction. However, after adjustment for the differences in the mean total skeleton weights by the analysis of covariance, the level of significance between the races is reduced ($P < 0.05$); the difference between the sexes and the interaction of race and sex are not significant.

The mean per cents contributed by the skeleton of the inferior limbs in each of the 4 groups to total skeleton weight are presented in table 2 and figure 3. In the White group, the inferior limbs of the male contribute a greater amount (46.0%) than of the female (44.0%). The percentage of total skeleton weight contributed by this division is greater in the Negro males (45.6%) than in the Negro females (42.2%). The analysis of variance shows that only the difference between the sexes is significant with the percentage contribution by the male being significantly greater ($P < 0.001$) than by the female.

Femurs

The mean weights of the femurs are presented in table 3 according to side,

TABLE 3

Means and standard deviations (S.D.) of the weights of the right and left femurs of and thei contributions in per cent to total skeleton weight according to race and sex

Race and sex	Weight in grams		Per cent of total skeleton weight	
	Mean	S.D.	Mean	S.D.
	Right femur			
White male	315.4	45.5	9.27	0.958
White female	205.4	50.9	8.90	0.890
Negro male	353.9	61.4	9.16	0.764
Negro female	236.6	57.2	8.34	0.890
	Left femur			
White male	320.1	41.8	9.40	0.736
White female	203.2	47.3	8.83	0.764
Negro male	355.2	58.8	9.20	0.577
Negro female	238.3	53.8	8.44	0.817

race, and sex. Since the difference between the weights of the right and left femurs is not significant in any of the 4 groups, the weights of the two sides were combined and tested for race and sex differences by the analyses of variance and covariance. The analysis of variance, shows the differences between races and between sexes to be significant ($P < 0.001$). However, after adjustment for differences in the mean total skeleton weights of the 4 groups in the analysis of covariance, the race difference is not significant but the sex difference remains highly significant ($P < 0.001$). Interaction between race and sex is not significant either before or after adjustment.

The mean per cents contributed by the right femur and by the left femur (table 3) of each of the 4 groups to total skeleton weight were tested separately. The percentage contribution by each femur to total skeleton weight is greater in the male than in the female and in the White than in the Negro groups. In all but the White female group the left femur contributes a slightly greater amount to the total skeleton weight than the right femur. By the analysis of variance, it is found that the right and the left femur each contributes significantly more ($P < 0.001$) to the total skeleton weight in the males than in the females; that the left femur, contributes significantly more ($P < 0.05$) in the White groups than in the Negro groups; and that the right femur contributes more in the White than in the Negro but with P merely approaching significance.

In order to compare the mean perc age contributions of the right and femurs to total skeleton weight a po error term based on the "Within gro variation for the right and left femur cents were used. The combining of t error terms is permissible since the m squares for the right and left femurs homogeneous. By the analysis of v ance, the mean square for the right left femur is less than the error term, th by showing no significant difference tween the relative amounts of total sk ton weight contributed by the two bo

DISCUSSION

The weight of human skeletons ma affected by many diverse factors. R sex, size, age and nutrition provide eff which are inherent characteristics of bones and constitute existent differen in weight which need to be known. effects of disease and of processes u in the preparation of the skeleton, maceration, degreasing, and drying, also alter the weight of the skeleton should be controlled. In this study, sk tons having evident pathology were cluded, and the preparation of the mate was uniform, i.e., all skeletons were pared by the same individual, using same technique. Reduction of the skele to a dry, fat-free state eliminated the ferences in moisture and fat content. mature skeletons with a wide and com able distribution of age among th groups were used. Nutrition effects unknown, but it may be relevant to

l the skeletons were from individu- ose remains had been assigned to atomical Board because of lack of for the usual disposition.

onsidering the results of this study ld be recalled that the concern is fferences in weight of the skeleton s parts between American Whites groes and between the sexes of each The absolute values are considered l as the relative contribution of a part to the total skeleton weight. obabilities associated with these dif- es are summarized in table 4.

Differences in the mean total skeleton weights of the 4 race-sex groups are significant with the Negro skeleton heavier than the White and the male skeleton heavier than the female.

The divisions of the skeleton which are found to account for race differences in the mean total skeleton weights are the superior and inferior limb skeletons (divisions III and IV). There is shown to be no significant race difference in the weights of vertebrae, ribs and sternum as a group (division II), and because of interaction between race and sex in the

TABLE 4

nmary of probabilities (P) in the analyses of variance and covariance associated with differences (race, sex, and interaction) in group means for total skeleton weight (TSW), for each division of the skeleton, and for femurs; and in the analysis of variance for differences among percentage contributions of each group to TSW

	Weights		Per cent contributions to TSW	
	Variance	Covariance	Analysis of variance	
	P	P	P	
al skeleton				
Groups	<0.001			
Race	<0.001			
Sex	<0.001			
Interaction	n.s.[1]			
Skull				
Groups	<0.001	n.s.	<0.001	
Race	n.s.	n.s.	n.s.	
Sex	n.s.	n.s.	<0.001	
Interaction	<0.05	<0.05	n.s.	
Vertebral column, ribs and sternum				
Groups	<0.001	<0.05	>0.05	
Race	<0.001	n.s.	n.s.	
Sex	<0.001	<0.001	<0.10	
Interaction	n.s.	n.s.	n.s.	
Superior limbs				
Groups	<0.001	<0.001	<0.001	
Race	<0.001	<0.01	<0.001	
Sex	<0.001	<0.001	<0.001	
Interaction	n.s.	n.s.	n.s.	
Inferior limbs				
Groups	<0.001	<0.05	<0.001	
Race	<0.001	<0.05	n.s.	
Sex	<0.001	n.s.	<0.001	
Interaction	n.s.	n.s.	n.s.	
			Right	Left
nurs				
Groups	<0.001	<0.001	<0.01	<0.001
Race	<0.001	n.s.	<0.10	<0.05
Sex	<0.001	<0.001	<0.001	<0.001
Interaction	n.s.	n.s.	n.s.	n.s.

Not significant.

weight of the skull, no conclusion could be reached concerning difference in weight of the skull between the two races or sexes.

In the mean weights of divisions II and III, the male is significantly heavier than the female; this difference cannot be accounted for by the greater skeleton weight of the male, as shown from the analysis of covariance.

The percentage contributions to the total skeleton weight by divisions I, III and IV are found to vary significantly between the sexes. The skull (division I) in the female of both races contributes a significantly greater amount to the total skeleton weight than in the male; however, the contributions by divisions III and IV are greater in the male than in the female. The only race difference in percentage contributions evident in this series is shown by division III (superior limbs). The relative contribution to the total skeleton weight by division II does not vary significantly between races or sexes, but the sex difference approaches the minimum probability level of significance used in this study. The sex difference present in the percentage contributions by inferior limbs is present also in the percentage contributions of the individual femurs; and, the left femur shows a significant race difference ($P < 0.05$) with the right femur approaching significance. It is of interest that significant differences are found in the percentage contributions to total skeleton weight among these 4 race-sex groups by a single bone, the femur, for which the percentage contributions range from 8% to 9%. There are no significant differences in percentage contributions between right and left femurs.

It is well known that the long limb bones are longer in Negroes than in Whites and in males than in females (Schultz, '37), and there is evidence also to indicate that the circumference and the amount of compact bone of the shaft of the femur are greater in the Negroes of both sexes than in the Whites (Merz, Trotter and Peterson, '56). The density (weight/volume) of the femurs and of the lumbar vertebrae is also significantly greater in the Negro than in the White, but no significant difference was found between the sexes (Bron Trotter and Peterson, '58). Thus, it is surprising to find that the total skeleto significantly heavier in the Negro t in the White and in the male than in female.

The relationships of the dependent v ables, the division weights, with the i pendent variable, total skeleton wei were tested and found to show linear gressions, i.e., an increase in the we of the division of the skeleton corresp to an increase in total skeleton weight, the same test applied to the relations of percentage contributions of each sion to total skeleton weight indicate significant change in the percentages increase in skeleton weight. Statis analyses used in determining differe among the 4 groups are more sens when applied to the actual weights tha the percentage contributions to the weight since in analyzing the percenta the range of variability is necessarily ited to 100%. In the levels of significa (table 4) of the contributions by race sex for weights (by the analysis of co iance) and for percentage contribution each of the 4 divisions (by the analysi variance) there is evident a general formity between the results of the tests excepting for the skull and for skeleton of the inferior limbs. The an sis of covariance of the weights of lower extremity shows a significant ference between races but not betw sexes, whereas the difference in per contributions to skeleton weight of lower extremity of the 4 groups is fo by the analysis of variance to be sig cant only between the sexes.

The study by Ingalls ('31) was car out on White male skeletons of the T Collection of which the source was cadaver material. The series was c posed of 100 skeletons, in contrast to 25 in the present White male series may be assumed that the chief differe between the skeletons used in the studies is that of fat-content and stat dryness. The Todd Collection skele had not been subjected to any degrea process and the weights were taken ordinary drying by air, whereas the s tons used in this study had been m

ghly dry and fat-free before weigh-
: is of interest to compare the results
se two White male series of similar

mean weight, 3418.7 gm, of the male skeletons used in this study is an that recorded by Ingalls, 4957 gm. ifference is probably due to the re- of fat from the present series rather o a difference in the overall size of eletons of the two series.

omparison between the percentage outions of the 4 arbitrary divisions l skeletal weight of the two series follows:

	Ingalls	Present study
	15	18.5
al column, nd sternum	19[1]	16.9
r limbs	19	18.5
: limbs	47	46.5

ermined from Ingalls' weight data.

lifference in the percentage con- ons by the same groups of bones en the two series might be explained : fact that in one series the bones lry and fat-free and in the other they not, since the relative proportion of ntent is not expected to be the same divisions of the skeleton.

s seen from this statistical study of ts of small series of male and female ons derived from two racial stocks significant differences are present, ly among the mean weights of the keleton of the 4 race-sex groups but mong the percentage contributions livision of the skeleton to the total on weight. It may be anticipated that racial stocks will likewise show dif- es. Thus, when weight is involved in ting the effect of a given external on the total skeleton by extrapola- rom measurement of a small part sultant error will be reduced if race x differences are taken into account.

SUMMARY AND CONCLUSIONS

-hundred dry, fat-free skeletons y divided among American Whites legroes of both sexes were selected wide and comparable age range in roup and for lack of gross pathology. The methods of preservation were known not to alter the skeleton. The bones were weighed individually with the exception of the bones of the cranium, hand, foot, ribs and moveable vertebrae. Each skeleton was divided into arbitrary divisions: (1) skull; (2) vertebrae, ribs and sternum; (3) superior limbs and (4) inferior limbs. The total skeleton weights, the weights of each division and the percentage contributions of each division to the total weight were studied. In addition, the femur weights were used in comparing a single bone weight to the total skeleton weight. The data were analyzed statistically in order to determine whether significant differences in the weights of the total skeleton, the 4 arbitrary divisions and the femurs, and in the percentage contribution of each division and of each femur to the total skeleton weight exist among the 4 groups.

A highly significant difference in the mean total skeleton weights of both races and sexes exists among the 4 groups. In both sexes, the mean total skeleton weight of the Negro is significantly heavier than in the White, and in both races, the male is significantly heavier than the female.

The mean weights of the superior and inferior limb skeletons are found to be significantly heavier in the Negro group than in the White group. The superior limbs are also significantly heavier in the male than in the female, but in the skeleton of the inferior limb no significant sex difference is present. The femurs are significantly heavier in the male than in the female with no significant race difference. In division II, the sex difference in the mean weights is highly significant, with no significant difference between the races. Because of the significant interaction between race and sex differences in the mean weight of the skull no conclusion can be reached concerning the source of the differences.

The contributions (in per cent) to the total skeleton weight by divisions I, III, and IV are found to vary significantly between the sexes. The relative contributions to the total skeleton weight by divisions III and IV are significantly greater in the male than in the female; however, in division I, the skull, the female contributes a significantly greater per cent to the total

skeleton weight than the male. Also, in division III, the Negro group contributes significantly more to the total skeleton weight than the White group. In division II, there are no significant differences among the 4 groups; but the difference between the sexes approaches the minimum probability level used in this study.

The relative amount of total skeleton weight contributed by the individual femurs is significantly greater in males than in females. The percentage contributions of the right and left femurs are greater in the White group than in the Negro group; for the left the difference is statistically significant, but for the right the difference merely approaches the 0.05 level of significance. There is no significant difference between the percentage contributions of right and left femur within a given group.

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.bution of Hereditary Blood Antigens Among the
ɪ and Non-Maya Indians in Mexico
Guatemala[1]

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.erous studies have been made on tribution of the hereditary blood in the ABO and M-N systems among of North America but comparative- work has been reported on Indians ral and South America. Compre- reviews on the North American have been prepared by Boyd ('39) re recently by Mourant ('54) and ant et al. ('58) and on South Amer- dies by Salzano ('57) and by Mour- al. ('58).

ugh some work has been done in various tribes of Indians in Mexico incidence of antigens in the ABO er, '30; Salazar-Mallen, '44; Sala- len and Martinez, '47; Wiener et al., eaga et al., '52), M-N (Wiener et Arteaga et al., '52), P (Wiener et) and Rh-Hr (Wiener et al., '45; . et al., '52), systems and in Guate- the ABO system (Cabrera, '50), nothing has been done in deter- the distribution among them of the cently discovered hereditary blood In view of this it was deemed im- to make a survey of the incidence e factors among Maya and non- dians of Mexico and Guatemala.

MATERIALS AND METHODS

ninary arrangements were made e United States Department of Education and Welfare, quarantine to permit the specimens which be sent in bond to the Minneapolis morial Blood Bank to pass through States Customs without intercep- the border. At Mexico City, permis- proceed with the project was by key men in appropriate depart- of the national government. Letters of introduction from the Instituto Nacional de Anthropologia e Historia, Instituto de Salubridad y Enfermedades Tropicales, Instituto Nacional Indigenista and from the Instituto de Historia at the University of Mexico, to the respective departments in the states visited, greatly facilitated the procurement of similar letters from the state authorities to the Presidente Municipal, health authorities and others in the communities where the specimens were obtained. The same procedure was followed in Guatemala. For the most part blood specimens were taken from the following tribes at hospitals, prisons and schools as well as clinics set up in the field:

Maya

In Mexico

1. Chol—15 specimens from San Cristobal, Las Casas, Chiapas.
2. Itza Maya—67 specimens from Merida and Xcopteil, Yucatan.
3. Lacandon—33 specimens from Rio Jatété and Monte Libano, Chiapas Jungle.
4. Tzeltal—111 specimens from San Cristobal, Las Casas, Chiapas. Aguacatenango and Monte Libano, Chiapas.
5. Tzotzil—91 specimens from Zinacantan, Chamula, Chilil and San Cristobal, Las Casas, Chiapas.

In Guatemala

1. Cakchiquel—9 specimens from Salola, Guatemala.
2. Mam—24 specimens from Huehuetenango and Quezeltenango, Guatemala.
3. Quiché Maya—203 specimens from Chichicastenengo, Quiché, Totonicapan and Quezeltenango, Guatemala.

Total Maya—553 specimens.

[1] This study was largely supported by research grant N.S.F. G-4573, National Science Foundation.

Non-Maya

In Mexico

1. Chiapaneca—41 specimens from Suchiapa and Tuxtla Gutierrez, Chiapas.
2. Mextizo—19 specimens from Papantla, Vera Cruz prison.
3. Totonaca—45 specimens from Papantla, Vera Cruz.
4. Zapoteca—143 specimens from Mitla and Tehuantepec, Mexico.

Total non-Maya—248 specimens. Total Maya and non-Maya specimens—801.

Blood specimens (5–8 cm^3) were taken from the median basilic vein by means of a sterile B-D vacutainer tube-needle assembly. Numbered labels had been put on each of the tubes. Each tube contained 0.17 ml of citric acid-dextrose solution. The specimens were refrigerated as soon as possible after they were taken and then shipped via air express in insulated shippers containing sealed bags of ice. The time in transit was usually less than 48 hours. The specimens arrived in excellent condition.

Upon arrival at the laboratory the blood samples were put at once in refrigeration at 4–6°C and the sera and clots were separated. Cells from the clots were tested with suitable antisera for A, B, M, N, S, D, C. E, c, e, P_1, K, Fy^a, Jk^a, Le^a, Le^b, Lu^a, Di^a, Mi^a, V and He antigens. Hemolysates were made from selected specimens for hemoglobin type studies. The serum specimens were numbered and placed in the deep freezer for future testing. Later the frozen serum specimens were sent to Dr. H. Eldon Sutton, Human Genetics Laboratory, University of Michigan Medical School, Ann Arbor, Michigan, to be tested for hereditary haptoglobins. The hemolysates were sent to Dr. R. W. Koucky, Fairview Hospital laboratory in Minneapolis for testing by paper electrophoresis method for hemoglobin types and later to Dr. Abner Robinson of the Child Research Center of Michigan, Detroit, Michigan, for confirmation by agar plate electrophoresis method. In this paper only the results of blood grouping tests will be reported, whereas the haptoglobin and hemoglobin studies will be reported in later publications.

RESULTS AND DISCUSSION

Only putatively full-blood Indians [i]cluded in this study. The custom o[f] dress and the word of the Indian h[.] was relied upon for determining the [.] of blood purity. However, informa[.] obtained may not in all instances [.] tirely accurate.

The results of the tests on the[.] specimens are listed in the tables [.] ing to the particular people und[.] blood group system considered. The[.] lation of the gene frequencies in [.] tables have been done by Whit[.] Johnson, Department of Mathemati[.] stitute of Technology, University o[.] nesota, using the recognized fo[.] outlined by Mourant ('54).

ABO blood groups

The results of the tests in the[.] system are shown on table 1.

From the table it is seen that [.] whole, both the Maya and non-Ma[.] dians are predominantly group O p[.] The O gene frequencies in 9 tribes o[.] ranged from 90.87% among 67 Itz[.] in Yucatan, Mexico, to 100% am[.] Cakchiquel in Guatemala. In the 4[.] of non-Maya, the O gene frequ[.] ranged from 81.95% in 41 Chiapa[.] 95.45% among 45 Totonaca. Th[.] centage frequency of the O gene [.] the 553 Maya is 96.80% as compa[.] the lower percentage frequency of 8[.] for the non-Maya group. The hi[.] quency of group O is in general [.] ment with previous studies among I[.] in Mexico (Arteaga et al., '52; Go[.] '30; Salazar-Mallen, '49, '44, '47; [.] et al., '45) and Guatemala (Cabrer[.] and with the larger body of India[.] mained in North (Boyd, '39; Brown[.] '58; Chown and Lewis, '53; Matso[.] Schrader, '33; Matson and Piper, '4[.] son et al., '54; Mourant, '54) and [.] America (Salzano, '57). In gener[.] more isolated peoples such as the [.] don, Tzeltal, Tzotzil and Cakchique[.] the highest frequency of the O ge[.] may be significant that according [.] dition the Itza Maya and the Chia[.] are reputed to be more mixed wit[.] Indian blood than are those group[.] have the higher gene frequencies [.]

TABLE 1

The ABO system

Peoples	Number tested	Number and per cent of phenotypes												Gene frequencies				Sum of gene frequencies
		O		A_1		A_2		B		A_1B		A_2B		r	p_1	p_2	q	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%					$r + p_1 + p_2 + q$
Maya																		
In Mexico																		
Chol	15	13	86.67	0	0.00	2	13.33	0	0.00	0	0.00	0	0.00	.9309	.0000	.0691	.0000	1.0000
Itza Maya	67	58	86.57	4	5.97	2	2.99	0	0.00	2	2.98	1	1.49	.9087	.0453	.0235	.0223	.9998
Lacandon	33	32	96.97	1	3.03	0	0.00	0	0.00	0	0.00	0	0.00	.9847	.0153	.0000	.0000	1.0000
Tzeltal	111	110	99.10	1	0.90	0	0.00	0	0.00	0	0.00	0	0.00	.9956	.0044	.0000	.0000	1.0000
Tzotzil	91	89	97.80	0	0.00	0	0.00	2	2.20	0	0.00	0	0.00	.9889	.0000	.0000	.0111	1.0000
In Guatemala																		
Cakchiquel	9	9	100.0	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1.0000	.0000	.0000	.0000	1.0000
Mam	24	22	91.67	2	8.33	0	0.00	0	0.00	0	0.00	0	0.00	.9574	.0426	.0000	.0000	1.0000
Quiché Maya	203	188	92.61	13	6.40	0	0.00	2	0.99	0	0.00	0	0.00	.9624	.0326	.0000	.0049	.9999
Total Maya	553	521	94.21	21	3.80	4	0.72	4	0.72	2	0.36	1	0.18	.9680	.0210	.0046	.0063	.9999
Non-Maya																		
In Mexico																		
Chiapaneca	41	27	65.85	8	19.51	1	2.44	5	12.20	0	0.00	0	0.00	.8195	.1034	.0138	.0633	1.0000
Mextizo	19	16	84.21	0	0.00	0	0.00	2	10.53	0	0.00	1	5.26	.8924	.0000	.0263	.0812	.9999
Totonaca	45	41	91.11	3	6.67	0	0.00	1	2.22	0	0.00	0	0.00	.9545	.0339	.0000	.0112	.9996
Zapoteca	143	109	76.22	18	12.59	3	2.10	12	8.39	0	0.00	0	0.00	.8731	.0688	.0113	.0465	.9997
Total non-Maya	248	193	77.82	29	11.69	4	1.61	20	8.07	1	0.40	1	0.40	.8814	.0624	.0108	.0454	1.0000

This suggests that the incidence of A and B antigen among any of these Indians is due to racial crossing. Examples of this are the relatively high frequencies for the B gene in the Mextizo, Chiapaneco and Zapoteca, the A_2 gene in the Chol, Itza Maya and Mextizo and the A_1 gene in the Itza Maya, Mam, Chiapaneco and Zapoteca.

Tradition asserts that the Chiapaneca Indians migrated many years ago into Chiapas from somewhere farther south in Nicaragua. It might be rewarding therefore, to study further the blood group distribution among this people as well as the Indians in Nicaragua, selecting as accurately as possible the full-bloods among them.

These observations are in general agreement with the findings in North American Indians which are group O except for the Blackfeet and related tribes in which there has been observed an equally high incidence of group A_1 (approximately 80%). (Matson, '33, '38; Matson and Schrader, '33; Matson et al., '36). This surprising high incidence of A_1 among the Blackfeet and related tribes, suggest the possibility of a relationship between some Amerinds and Polynesians in whom also there is a high incidence of group A_1 (60.8%): (Nigg, '30; Simmons and Graydon, '57). Indeed Heyerdahl ('50, '52) suggests that the early inhabitants of Polynesia could have been carried in small craft by ocean currents and prevailing winds from the west coast of South America to the Polynesian Islands of the Pacific.

The Winnebago Indians also have a higher incidence of group A_1 (approximately 42%) than is found among the general body of full-blood Indians and is higher than can be accounted for on the basis of white admixture (Matson, '41). Close proximity and intermarriage with the group A_1 Blackfeet earlier in their history, perhaps in the Hudson's Bay area, could explain the high incidence of group A_1 among the Winnebago.

The MN-Ss system

Tests for the M and N antigens were done by the slide technique with commerical antisera. The reagents were potent and specific giving satisfactor[y re]actions with known control bloods. [The] results of the tests are shown on ta[ble 2].

From table 2 it is apparent tha[t the] expected high incidence of M amon[g In]dians prevails among these Indians. [The] percentage frequency of the M gene r[anges] from 61.11% among the Cakchiqu[el to] 86.67% among the Chol and Toto[naca]. There is not much difference in the [per]centage incidence of the M gene a[mong] the Maya and the non-Maya groups. [The] frequency in the former being 75[%] and in the latter group 72.58%. [This] agrees with the unusually high incid[ence] of M among other Indians tested in [Cen]tral America (Arteaga et al., '52; W[iener] et al., '45) in North America (Boyd[,] Brown et al., '58; Chown and Lewis[,] Levine et al., '35; Matson and Piper[,] Matson and Roberts, '49; Matson e[t al.,] '36, '54; Pantin and Kallsen, '53) [in] South America, (Salzano, '57; Mo[...] et al., '58) as compared to whites [and] other races (Landsteiner and Levine, [...]

Anti-s serum was not available [and] therefore the bloods were tested with [anti-] S serum only. Control tests of the s[erum] were done using standard bloods o[f all] groups and these gave satisfactory re[sults]. Because of a limited quantity of S [anti]body reagent the S antigen was determ[ined] on only 169 blood specimens. Thes[e re]sults are shown on table 3.

As seen from table 3 these speci[mens] were obtained from 109 Maya an[d ...] non-Maya Indians in Mexico. The t[ribes] have a gene frequency of S varying [from] 28.51% among 45 Totonaca to 55.[...] among 15 Mextizo tested. The per[centage] frequency of the S gene in the Ma[ya is] 40.18% and for the non-Maya 34.1[...]. Except for the Mextizo and Tzeltal, [the] latter in which the S gene frequenc[y is] 47.78%, these values do not differ m[uch] from 34.2% reported for pure Chipp[ewa] (Matson et al., '54) and 38.2% for [the] Blood tribe (Chown and Lewis, '53). [Nei]ther do the values differ greatly from [the] per cent gene frequency of S for a w[hite] population in the United States as repo[rted] by Levine, et al., '51 (34.9%) or [for] Englishmen as reported by Race and [San]ger, '58 (32.7%) or from our finding[s]

TABLE 2

Mn system

Peoples	Number tested	Number and per cent of phenotypes						Gene frequencies		Sum of gene frequencies
		M		MN		N		M	N	
		No.	%	No.	%	No.	%			
Maya										
In Mexico										
Chol	15	11	73.33	4	26.67	0	0.00	0.8667	0.1333	1.0000
Itza Maya	67	34	50.75	25	37.31	8	11.94	0.6940	0.3060	1.0000
Lacandon	33	23	69.70	8	24.24	2	6.06	0.8182	0.1818	1.0000
Tzeltal	111	69	62.16	39	35.14	3	2.70	0.7973	0.2027	1.0000
Tzotzil	91	53	58.24	30	32.97	8	8.79	0.7473	0.2527	1.0000
In Guatemala										
Cakchiquel	9	3	33.33	5	55.56	1	11.11	0.6111	0.3889	1.0000
Mam	24	13	54.17	11	45.83	0	0.00	0.7708	0.2292	1.0000
Quiché Maya	203	112	55.17	74	36.46	17	8.37	0.7340	0.2659	0.9999
Total Maya	553	318	57.50	196	35.44	39	7.05	0.7523	0.2477	1.0000
Non-Maya										
In Mexico										
Chiapaneca	41	19	46.34	15	36.59	7	17.07	0.6463	0.3537	1.0000
Mextizo	19	10	52.63	6	31.58	3	15.79	0.6842	0.3158	1.0000
Totonaca	45	35	77.78	8	17.78	2	4.44	0.8667	0.1333	1.0000
Zapoteca	143	77	53.85	49	34.26	17	11.89	0.7098	0.2902	1.0000
Total Non-Maya	248	141	56.85	78	31.45	29	11.69	0.7258	0.2742	1.0000

TABLE 3

S-s system

Peoples	Number tested	Number and per cent of phenotypes				Gene frequencies		Sum of gene frequencies
		SS & Ss		s		S	s	
		No.	%	No.	%			
Maya								
In Mexico								
Itza Maya	62	39	62.90	23	37.10	0.3909	0.6091	1.0000
Tzeltal	22	16	72.73	6	27.27	0.4778	0.5222	1.0000
Tzotzil	25	15	60.00	10	40.00	0.3675	0.6325	1.0000
Total Maya	109	70	64.22	39	35.78	0.4018	0.5982	1.0000
Non-Maya								
In Mexico								
Mextizo	15	12	80.00	3	20.00	0.5528	0.4472	1.0000
Totonaca	45	22	48.89	23	51.11	0.2851	0.7149	1.0000
Total Non-Maya	60	34	56.67	26	43.33	0.3417	0.6583	1.0000

TABLE 4

MN Ss system

Peoples	Number tested	Number and per cent of phenotypes												Chromosome frequencies				Sum of gene frequencies
		MS		Ms		MNS		M_sN_s		NS		Ns		MS	Ms	NS	Ns	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%					
Maya																		
In Mexico																		
Itza Maya	62	17	27.42	15	24.19	16	25.81	7	11.29	6	9.68	1	1.61	0.2042	0.4898	0.1868	0.1192	1.0000
Tzeltal	22	4	18.18	5	22.72	11	50.00	1	4.55	1	4.55	0	0.00	0.2030	0.5943	0.2027	0.0000	1.0000
Tzotzil	25	6	24.00	7	28.00	6	24.00	3	12.00	3	12.00	0	0.00	0.1148	0.6325	0.2527	0.0000	1.0000
Total Maya	109	27	24.77	27	24.77	33	30.28	11	10.09	10	9.17	1	0.92	0.2278	0.5245	0.1741	0.0736	1.0000
Non-Maya																		
In Mexico																		
Mextizo	15	7	46.67	1	6.67	3	20.00	2	13.33	2	13.33	0	0.00	0.2370	0.4472	0.3158	0.0000	1.0000
Totonaca	45	18	40.00	17	37.78	3	6.67	5	11.11	1	2.22	1	2.22	0.2483	0.6184	0.0368	0.0965	1.0000
Total Non-Maya	60	25	41.67	18	30.00	6	10.00	7	11.67	3	5.00	1	1.67	0.2163	0.5095	0.1254	0.1488	1.0000

mong whites in Minnesota (Mat-
l., '54).
istribution of the S-s antigen in
to the three genotypes MM, MN
and the corresponding frequency
chromosomes MS, Ms, NS and Ns
n on table 4.
table 4 it may be observed that
Maya and the Mextizo show an
bly smaller frequency of Ms than
tively purer Totonaca (44.72%
34% respectively). However, to
degree the same appears to be true
tza Maya of Yucatan.
hromosome frequencies for Maya
-Maya on table 4 are shown on
with similar data from other stud-
omparison.
ifferences are not great between
groups of Indians with regard to
Ms but the NS is high compared
nong the Maya whereas among the
a there is a more equitable dis-
of these chromosomes. The fre-
of the NS appears to be high for
s tested in this study and, with the
n of Chown's ('53) findings in
d tribe, Ns is lower than among
dians (Brown et al., '58; Matson
4; Pantin and Kallsen, '53) and
ish (Race and Sanger, '58).

he Henshaw (He) antigen

ted amount of anti-He serum was
ailable to us for this study through
ness of Dr. T. J. Greenwalt of
ee Blood Center, Milwaukee, Wis-
The antiserum was satisfactory
eaction with known He positive
A total of 166 Maya (67 Itza
7 Tzeltal and 62 Tzotzil) and 80
a (45 Totonaca, 20 Zapoteca and
izo) bloods were tested. No He
was found among these 246
s.
e antigen appears to be typically
character (Chalmers et al., '53;
l Mourant, '51). Among 1,423
icans it was found in 38 (2.7%).
ot found in 1,500 Whites (Chal-
al., '53). The He gene is closely
bsolutely linked with the MNSs
Nijenhuis, '53; Shapiro, '56; Zou-
'55). The gene responsible for
haw (He) phenotype appears to
be rare if present at all among the Amerinds tested.

The Miltenberger (Mi^a) antigen

We had available some potent anti-Mi^a serum obtained in Minneapolis from a group O donor sensitized through pregnancy. The serum was not absorbed and was usable therefore only on group O bloods. This, however, was of little hindrance in this study of preponderantly group O people. Although the anti-Mi^a serum reacted well with Mi(a+) controls, it is presumed that it contained some anti-Vw as well, since anti-Mi^a sera tested so far are considered to contain also, anti-Vw (Race and Sanger, '58). No Mi^a antigen was found in the 521 Maya and 193 non-Maya group O Indians tested.

The Mi(a+) phenotype is rare among white people (one in about 500) and it has become evident that the gene or genes responsible for phenotypes Mi(a+)Vw+ and Mi(a+)Vw–, are linked to the MNSs genes (Hart et al., '54; Wallace et al., '57). The absence of cross-overs in families suggests a very close linkage. It has also been observed that usually the gene or genes responsible for the Mi(a+)Vw+ reaction are accompanied by N and s, while those responsible for the Mi(a+)Vw– reaction are accompanied by M and S (Race et al., '51). Since the incidence of N is small among Indians, the chance of finding Mi(a+)Vw+ among them would be correspondingly small, if indeed the Mi^a and Vw genes exist at all in pure Amerinds.

The P system

Recent work on the P system by Sanger ('55) and more recently by Matson, Swanson, Noades, Sanger and Race ('58) has made some revolutionary changes in the concept of this system. The newer notations P_1 and P_2 are used in this paper, where P_1 is the antigen previously called P and P_2 is the one formerly called p.

Only anti-P_1 (anti-P) sera were used in testing the bloods, one a commercially distributed fluid reagent and one dried antiserum obtained through the kindness of Dr. A. E. Mourant, Lister Institute, London, England. Weak and doubtful reactions were checked with a rather potent

TABLE 5

The MN-Ss chromosome frequencies

Peoples	MS	Ms	NS	Ns
Maya (this study)	22.78	52.45	17.41	7.36
Non-Maya (this study)	21.63	50.95	12.54	14.88
Chippewa (Matson, Koch and Levine, '54)	29.60	42.40	4.60	23.40
Blood (Chown and Lewis, '53)	30.10	56.50	6.90	6.50
Diegueno (Pantin and Kallsen, '53)	40.10	35.50	0.00	24.40
West Navaho (Brown et al., '58)	14.40	41.60	23.23	20.77
Pima (Brown et al., '58)	13.27	57.07	10.94	18.71
English (Race and Sanger, '58)	24.70	28.30	8.00	39.00

TABLE 6

P system[1]

Peoples	Number tested	Number and per cent of phenotypes				Gene frequencies		Sum of gene frequencies
		P_1+		P_1-		P_1	P_2	
		No.	%	No.	%			
Maya								
In Mexico								
Chol	15	9	60.00	6	40.00	0.3675	0.6325	1.0000
Itza Maya	67	45	67.16	22	32.84	0.4270	0.5730	1.0000
Lacandon	33	24	72.73	9	27.27	0.4778	0.5222	1.0000
Tzeltal	101	68	67.33	33	32.67	0.4284	0.5716	1.0000
Tzotzil	75	54	72.00	21	28.00	0.4708	0.5292	1.0000
Total Maya	291	200	68.73	91	31.27	0.4408	0.5592	1.0000
Non-Maya								
In Mexico								
Mextizo	16	12	75.00	4	25.00	0.5000	0.5000	1.0000
Totonaca	45	27	60.00	18	40.00	0.3675	0.6325	1.0000
Zapoteca	43	28	65.12	15	34.88	0.4094	0.5906	1.0000
Total Non-Maya	104	67	64.42	37	35.58	0.4035	0.5965	1.0000

[1] Tested with anti-P_1 only

une human anti-P_1 serum prepared
ur laboratories. Positive and negative
rols were employed as reference. Be-
e of the scarcity of anti-P_1 only 291
a and 104 non-Maya bloods were
d. The results are shown on table 6.
here do not appear to be any outstand-
differences in the distribution of P_1
veen Maya and non-Maya Indians.
her do large differences appear be-
n tribes within each group. The per-
age incidence of P_1 among the 291
a is 68.73% and among 104 non-Maya
4.42%. Assuming the P_1 negatives
e P_2 the percentage of gene frequencies
the Maya were calculated at 44.08%
P_1 and 55.92% for P_2 and for the non-
a 40.35% for P_1 and 59.65% for P_2.
omparing these findings with the
notype per cent for pure Chippewa
tson et al., '54) we find them to be
ewhat lower, the Chippewa having
% P. Chown and Lewis ('53) also
rted 85% P for the Blood Indians.
vever, Pantin and Junqueira ('52)
nd only 41.1% P among 73 Brazilian
ans and Pantin and Kallsen ('53) re-
57% among 58 Dieguenos. A study
300 Whites in Minnesota (Matson et
'54) showed 79.70% P which does not
greatly from that found among the
ppewa (Matson et al., '54) and Bloods
own and Lewis, '53).

The Rh-Hr system

resented on tables 7 and 8 are the
lts of Rh and hr tests using the 5
sera, anti-C, anti-D, anti-E, anti-c and
-e. These anti-sera were continually
cked for potency and specifiicity. Slide
ng tests were performed on all the
d specimens and doubtful reactions
e re-checked by a tube test using anti-
of a different lot or from a different
nufacturer. A slide control was run
each blood to rule out false positives
to rouleaux, auto-agglutination, con-
ination, etc. Anti-D, anti-E and anti-c
e prepared in our own laboratorioes,
ereas the remaining antisera were ob-
ed from various commercial distribu-
. The anti-C and anti-e gave generally
ker reactions and frequently the re-
s were questioned and the tests re-
ted. Owing to the scarcity of anti-e sera, these determinations were done only on bloods possessing the E factor. The chromosome frequencies were computed by the formulae of Mourant ('54). These formulae are considered by Boyd ('54, '54a) to be the most accurate of the simple methods for determining Rh-hr chromosome frequencies.

From table 8 it can be seen that both the Maya and non-Maya Indians have a high chromosome frequency of CDe(R^1) and cDE(R^2) a low incidence of cde(r) and cDe(R^0) and in most tribes (Chol, Tzotzil, Cakchiquel, Quiché Maya, Chiapaneca, Totonaca and Zapoteca) there is some CDE(R^z). No homozygous cDe(Rh_o) or cde(rh) were observed in the Maya Indians. Only one Rh negative appeared in the non-Maya group, this in the Chiapaneca (table 7). In the absence of homozygotes there is no way of knowing whether cDe or cde is present. These are listed, therefore, as cDe and/or cde. It is more likely, however, that the chromosome frequency is entirely cde since phenotype ccDee occurs rarely in Amerinds. The calculated cDe and/or cde chromosome frequency for the Chol is extremely high, but this could easily be due to the small sampling and the fact that two brothers in this group appear to have the cDe or cde chromosome. The relatively higher frequencies for cDe and/or cde for the Chol, Itza Maya, Mam, Chiapaneca, Totonaca and Zapoteca series suggest rather extensive admixture.

It may be noteworthy that the Lacandon (Wilson, '48) who have isolated themselves for centuries from whites and other Indians and in whom there is a considerable amount of inbreeding and incest, show an extremely high frequency of the cDE chromosome (65.15%) (table 8). On the other hand, the Cakchiquel show 70.15% frequency for CDe. In the latter tribe also, two siblings appear to be CDE/CDe. It is to be expected in a people having a high cDE that this would be accompanied by moderate values of cdE. However, due to the extremely high incidence of D, and the absence of dd individuals this chromosome could not be demonstrated.

A high cDE and low cde has been reported by Matson, Koch and Levine ('54)

TABLE 7

Rh-hr system

Peoples	Number tested	Number and per cent of phenotypes[1]															
		CCDEe		CCDee		CcDEE		CcDEe		CcDee		ccDEE		ccDEe		ccddee	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Maya																	
In Mexico																	
Chol	15	1	6.67	3	20.00	0	0.00	5	33.33	1	6.67	4	26.66	1	6.67	0	0.00
Itza Maya	67	0	0.00	16	23.88	0	0.00	32	47.76	5	7.46	5	7.46	9	13.44	0	0.00
Lacandon	33	0	0.00	4	12.12	1	3.03	14	42.42	0	0.00	13	39.39	1	3.03	0	0.00
Tzeltal	111	0	0.00	30	27.03	0	0.00	47	42.34	7	6.30	21	18.92	6	5.41	0	0.00
Tzotzil	91	5	5.49	22	24.18	1	1.09	45	49.45	3	3.30	12	13.19	3	3.30	0	0.00
In Guatemala																	
Cakchiquel	9	2	22.22	4	44.45	0	0.00	3	33.33	0	0.00	0	0.00	0	0.00	0	0.00
Mam	24	0	0.00	7	29.17	0	0.00	10	41.66	1	4.17	3	12.50	3	12.50	0	0.00
Quiché Maya	203	4	1.97	67	33.00	3	1.48	87	42.86	5	2.46	31	15.27	6	2.96	0	0.00
Total Maya	553	12	2.17	153	27.67	5	0.90	243	43.94	22	3.98	89	16.09	29	5.24	0	0.00
Non-Maya																	
In Mexico																	
Chiapaneca	41	1	2.44	12	29.27	0	0.00	18	43.90	4	9.76	2	4.88	3	7.31	1	2.44
Mextizo	19	0	0.00	7	36.84	0	0.00	8	42.11	1	5.26	2	10.53	1	5.26	0	0.00
Totonaca	45	2	4.44	12	26.67	0	0.00	16	35.55	4	8.89	8	17.78	3	6.67	0	0.00
Zapoteca	142	1	0.70	26	18.31	0	0.00	62	43.66	23	16.20	21	14.79	9	6.34	0	0.00
Total Non-Maya	247	4	1.62	57	23.08	0	0.00	104	42.11	32	12.96	33	13.36	16	6.48	1	0.40

[1] None of the following phenotypes were observed: CCDEE, CCddEE, CCddEe, CCddee, CcddEE, CcddEe, Ccddee, ccDee, ccddEE, ccddEe.

TABLE 8

Rh-Hr chromosome frequencies

Peoples	Number tested	R^z CDE	R^1 CDe	R^y CdE	r' Cde	R^2 cDE	r'' cdE	R^o cDe and/or r cde
Maya								
In Mexico								
Chol	15	0.0745	0.3921	0.0000	0.0000	0.2921	0.0000	0.2412
Itza Maya	67	0.0000	0.5149	0.0000	0.0000	0.3806	0.0000	0.1045
Lacandon	33	0.0000	0.3485	0.0000	0.0000	0.6515	0.0000	0.0000
Tzeltal	111	0.0000	0.5135	0.0000	0.0000	0.4279	0.0000	0.0586
Tzotzil	91	0.0559	0.5101	0.0000	0.0000	0.3782	0.0000	0.0558
In Guatemala								
Cakchiquel	9	0.0167	0.7055	0.0000	0.0000	0.2611	0.0000	0.167
Mam	24	0.0000	0.5208	0.0000	0.0000	0.3958	0.0000	0.0834
Quiché Maya	203	0.0171	0.5666	0.0000	0.0000	0.3893	0.0000	0.0270
Total Maya	553	0.0206	0.5219	0.0000	0.0000	0.4061	0.0000	0.0514
Non-Maya								
In Mexico								
Chiapaneca	41	0.0225	0.5628	0.0000	0.0000	0.2945	0.0000	0.1201[1]
Mextizo	19	0.0000	0.6053	0.0000	0.0000	0.3421	0.0000	0.0526
Totonaca	45	0.0430	0.4903	0.0000	0.0000	0.3681	0.0000	0.0986
Zapoteca	142	0.0823	0.4706	0.0000	0.0000	0.3506	0.0000	0.0965
Total Non Maya	247	0.0169	0.5054	0.0000	0.0000	0.3678	0.0000	0.1100

[1] Most probably r.

TABLE 9

Rh-Hr chromosome frequencies in Maya and non-Maya Indians compared with other Indians

Peoples	Number tested	CDE R^z	CDe R^1	cDE R^2	cDe R^o	Cde r'	cdE r''	cde r
Maya (this study)	553	0.0206	0.5219	0.4061	0.0514[1]	0.0000	0.0000	0.0000
Non-Maya (this study)	247	0.0169	0.5054	0.3678	0.1100[1]	0.0000	0.0000	0.1210[1]
Chippewa (Matson et al., '58)	161	0.0190	0.3150	0.5870	0.0000	0.0000	0.0790	0.0000
Blood (Chown and Lewis, '53)	241	0.0383	0.4689	0.4011	0.0000	0.0000	0.0269	0.0648
Navaho (Brown et al., '58)	104	0.0260	0.3753	0.2605	0.3382[1]	0.0000	0.0000	0.0000

[1] The calculations did not segregate this value into R^o and r. It may be one or the other or both may be included.

TABLE 10

The antigen V: phenotype and gene frequencies in Indians of Central America compared to other peoples

Peoples	Investigator	Number tested	Per cent of phenotypes		Per cent of gene frequencies	
			V+	V−	V	v
Central American Indians	This study	801	0.13	99.87	0.36	99.64
Negroes (West Africa)	DeNatale et al., '55	150	40.00	60.00	22.54	77.46
Negroes (New York City)	DeNatale et al., '55	168	26.79	73.21	14.44	85.56
Negroes (Seattle)	Giblett et al., '57	327	28.75	71.25	15.59	84.41
Whites (London)	DeNatale et al., '55	407	0.49	99.51	0.25	99.75
Whites (Seattle)	Giblett et al., '57	514	0.19	99.81		
Orientals	Giblett et al., '57	272	0.37	99.63		
North American Indians	Giblett et al., '57	174	1.15	98.85		

· the Chippewa; Chown and Lewis ('53) · the Blood tribe; Wiener et al. ('45) for ; Mexican Indians; Matson and Piper ·7) for the Ute tribe; Matson and Rob-s ('49) for Eskimos in Western Alaska; ntin and Kallsen ('53) for Diegueno d Pima Indians and Brown et al. ('58) · Navaho, Apache and other Indians in izona.

The results of this study as compared :h those done on other putatively full ›oded Amerinds of North America are nmarized in table 9.

Aside from the specific difference noted ›ve, the findings among the Maya and n-Maya in this study appear to be in ıeral agreement with those found ıong other tribes of Indians and Eski-›s (Brown et al., '58; Landsteiner et al., ; Matson and Piper, '47; Matson and berts, '49; Wiener et al., '45) and differ m whites in the same respects, i.e., a ;h cDE, a low incidence or absence of e and cde and the presence of CDE :omosomes. Indeed the outstanding :ture is the high frequency of the r″(E) ıe among Indians wherein they surpass other known populations except per-ps the Polynesians. Generally speaking : Rh factor is high also among other n-European peoples, e.g., the Chinese, evine and Wong, '43; Wiener et al., '44) lonesians and Aborigines of Australia d the Pacific Islands (Sanger et al., ; Simmons et al., '44, '45, '48).

Incidence of the V antigen

A very good anti-V serum was obtained this study through the kindness of Dr. R. Giblett, King County Blood Bank, ıttle, Washington. This serum was ab-bed and suitable for testing bloods of groups. V positive and V negative ›ods served as satisfactory controls.

All of the 801 specimens of Maya and ı-Maya blood were tested with this an-:rum and all but one (a Totonaca) were ınd to lack the V antigen. This was re or less to be expected since the gene so far has been traced only in the chro-somes cDef and cdef and these chro-somes were found to be rare in the In-ns tested, as indeed they have been ınd to be rare in all Amerinds.

For the incidence of the V antigen and the frequency of its gene in groups of people we are indebted principally to two studies. De Natale et al. ('55) reported on the incidence of V in West Africans, Negroes in New York and Whites in London and Giblett et al. ('57) provided further figures for Negroes in Seattle Caucasians, Orientals and American Indians. These data are tabulated on table 10.

Lutheran system

Tests for Lutheran groups were limited to the use of anti-Lu^a serum. Two anti-Lu^a sera were made available to us for this study. One from Dr. Tibor Greenwalt, Milwaukee Blood Center, Milwaukee, Wisconsin had the other from Dr. A. E. Mourant, Lister Institute, London, England. The Milwaukee serum was from a group O donor and was not absorbed. The Lister serum was usable for all groups. Both antisera reacted not strongly but still satisfactorily with positive control bloods and it was completely negative with negative controls.

No Lu(a+) phenotype was found in any of the 173 Maya (three tribes—67 Itza Maya, 37 Tzeltal and 69 Tzotzil) or 109 non-Maya (three tribes—45 Totonaca, 49 Zapoteca and 15 Mextizo) Indians tested with the available antisera, thus giving a frequency of 100% for the Lu^b gene (homozygous $Lu^b Lu^b$). This agrees with the findings of Chown and Lewis ('53) among 97 Blood Indians in Alberta and among 25 Eskimos. To our knowledge the only reported Lu^a positives in Amerinds were those reported by Pantin and Kallsen ('53) among 58 Diegueno Indians in California (3.45% Lu(a+) phenotype, 1.74% Lu^a gene) and by Pantin and Junqueira ('52) among 73 Brazilian Indians (16.44% Lu (a+) phenotype, 8.59% Lu^a gene). The Lu^a gene is rare or does not appear at all in Asian peoples that have been studied, (South India, Lehmann and Cutbush, '52; Malaya and Borneo, Pelunin and Sneath, '53). Peoples of Western Europe have a higher incidence of Lu(a+). In a study representative of Caucasians, Callender and Race ('46) report 7.90% Lu(a+) or a frequency of 4.03% for the Lu^a gene in 582 English.

TABLE 11

Kell system

Peoples	Number tested	Number and per cent of phenotypes				Gene frequencies		Sum of gene frequencies
		K+[1]		K–		K	k	
		No.	%	No.	%			
Maya								
In Mexico								
Chol	15	0	0.00	15	100.00	0.0000	1.0000	1.0000
Itza Maya	67	1	1.49	66	98.51	0.0075	0.9925	1.0000
Lacandon	33	0	0.00	33	100.00	0.0000	1.0000	1.0000
Tzeltal	111	2[2]	1.80	109	98.20	0.0091	0.9909	1.0000
Tzotzil	91	0	0.00	91	100.00	0.0000	1.0000	1.0000
In Guatemala								
Cakchiquel	9	0	0.00	9	100.00	0.0000	1.0000	1.0000
Mam	24	0	0.00	24	100.00	0.0000	1.0000	1.0000
Quiché Maya	203	0	0.00	203	100.00	0.0000	1.0000	1.0000
Total Maya	553	3	0.54	550	99.46	0.0027	0.9973	1.0000
Non-Maya								
In Mexico								
Chiapaneca	41	1	2.44	40	97.56	0.0123	0.9877	1.0000
Mextizo	19	0	0.00	19	100.00	0.0000	1.0000	1.0000
Totonaca	45	0	0.00	45	100.00	0.0000	1.0000	1.0000
Zapoteca	141	3	2.13	138	97.87	0.0107	0.9893	1.0000
Total Non-Maya	246	4	1.63	242	98.37	0.0082	0.9918	1.0000

[1] Tested with anti-k sera. No KK were found.

[2] Brothers.

The Kell-Cellano system

All the blood specimens were tested for e Kell antigen using a reliable anti-Kell rum prepared in our laboratory from nsitized donors. Only K positive specins were tested with anti-k. The findings e shown on table 11.

Nearly all the Indians tested were Kell gative, presumably homozygous Cellano sitive. No homozygous KK were found. ree Kk individuals were observed in 553 aya (two of these are brothers) and 4 Kk re observed in the 248 non-Maya. One ay conclude that the Kell gene is extremerare among these Indians and when und is probably indicative of white adxture. The gene frequencies for the 553 aya were 0.27% for the Kell gene and .73% for the k gene. For the non-Maya e gene frequency for Kell appears to be a tle higher, 0.82% and 99.18% for the k ne.

These findings are in general agreement th values reported by others for Inans (Chown and Lewis, '53, '57; Matson al., '54), however, Pantin and Junqueira 52) report a value of 12.41% for the gene among 73 Brazilian Indians. The equency for the Kell gene among whites Manitoba has been reported recently ewis et al., '55) to be 6.9%.

The Lewis system

Antisera used in testing for Le^a and ^{b} antigens were prepared at the Minapolis War Memorial Blood Bank. Three ti-Le^a, one anti-Le^b and one anti-Le^a + ^{b} were used. The antisera appeared to potent and specific. Though the blood ecimens arrived in good condition for ouping, it should be pointed out that e Lewis antigens are fragile and give eir best reactions when blood is freshly awn. Saliva specimens were not obinable for study.

The Lewis system is still obscure in me of its aspects and the genetics of e system are uncertain. Gene frequenes cannot be calculated with confidence Aourant, '54) and therefore the incince of Lewis groups are reported on ble 12 only in terms of the number and r cent of phenotypes.

The Le(a+b−) group is rare among these Indians. Only 6 or 1.08% were found among the 553 Maya and only 5 or 2.04% were observed among the 245 non-Maya. The Le(a−b+) was the most common phenotype ranging from 55.50% among 9 Cakchiquels to 82.22% among 45 Totonacas. The percentage phenotypes for the 553 Maya was 77.40% and of the 245 non-Maya 171 or 69.80% were group Le(a−b+). Absence of both the Le^a and Le^b antigens was noted in 119 or 21.52% of the Maya and in 69 or 28.16% of the non-Maya.

Only a few other studies have been reported for the distribution of the Lewis antigens among Amerinds. Chown and Lewis ('53) included in their series tests on 39 Blackfeet and 241 Bloods of all of whom lacked the Le^a antigen. In 1949, Salazar-Mallen ('49) reported on 81 Otomis Indians and 199 Mexicans in whom he found 9.88% to be Le(a+) and 90.12% to be Le(a−). The Mexicans were found to be 11.56% Le(a+) and 88.44% Le(a−). Arteaga et al. ('52) reported 12.06% Le(a+) for 141 Mexicans in Mexico City.

Studies in which both anti-Le^a and anti-Le^b were used reveal differences between these Indians in Central America and other peoples that have been studied. Among other peoples there is generally more Le(a+b−) and less Le(a−b−) with the exception of Swedes (Grubb, '51), Greeks (Mourant, '54), West African Negroes (Barnicot and Lawler, '53) and American Negroes (Miller et al., '51) (see table 13). For the most part however, peoples of western Europe (Allison et al., '52; Andresen, '48; Mourant, '54), Chinese (Miller et al., '51), Maori (Simmons et al., '51), Australian Whites (Simmons and Jacobowicz, '51) and American Whites (Miller et al., '51) are low in Le(a−b−).

The Duffy (Fy^a) system

The Duffy factor among these Indians was determined only with anti-Fy^a sera since these were the only ones available to us. Commercial antisera from two manufacturers were used and these appeared to be satisfactory when tested with

TABLE 12

The Lewis system

Peoples	Number tested	Number and per cent of Lewis phenotypes							
		Le(a+b–)		Le(a–b+)		Le(a–b–)		Le(a+b+)	
		No.	%	No.	%	No.	%	No.	%
Maya									
In Mexico									
Chol	15	0	0.00	12	80.00	3	20.00	0	0.00
Itza Maya	67	0	0.00	54	80.60	13	19.40	0	0.00
Lacandon	33	0	0.00	23	69.70	10	30.30	0	0.00
Tzeltal	111	1	0.90	84	75.68	26	23.42	0	0.00
Tzotzil	91	2	2.20	73	80.22	16	17.58	0	0.00
In Guatemala									
Cakchiquel	9	0	0.00	5	55.56	4	44.44	0	0.00
Mam	24	1	4.17	18	75.00	5	20.83	0	0.00
Quiché Maya	203	2	0.98	159	78.33	42	20.69	0	0.00
Total Maya	553	6	1.08	428	77.40	119	21.52	0	0.00
Non-Maya									
In Mexico									
Chiapaneca	41	0	0.00	27	68.85	14	34.15	0	0.00
Mextizo	19	0	0.00	15	78.95	4	21.05	0	0.00
Totonaca	45	0	0.00	37	82.22	8	17.78	0	0.00
Zapoteca	140	5	3.57	92	65.72	43	30.71	0	0.00
Total Non-Maya	245	5	2.04	171	69.80	69	28.16	0	0.00

TABLE 13

Samples tested with anti-Le^a and anti-Le^b (Lewis groups)[1]

Peoples	Investigator	Number tested	Per cent of phenotypes			
			Le(a+b−)	Le(a−b+)	Le(a−b−)	Le(a+b+)
English	Ikin et al. (in Mourant, '54)	1166	21.10	71.61	7.29	0.00
Norwegian Lapps	Allison et al., '52	90	8.89	81.11	10.00	0.00
Swedes	Grubb, '51	1000	18.70	52.60	28.70	0.00
Danes	Andresen, '48	238	19.33	74.79	5.88	0.00
Greeks (Athens)	Dunsford, (in Mourant, '54)	34	11.76	55.88	32.35	0.00
West African Negroes	Barnicot and Lawler, '53	105	17.14	43.81	39.05	0.00
Chinese (New York)	Miller et al., '51	85	23.53	69.41	5.88	1.18
Maori	Simmons et al., '51	71	21.13	60.56	7.04	11.27
Australian Whites	Simmons and Jakobowicz, '51	500	26.40	69.80	3.60	0.20
American Negroes	Miller et al., '51	200	23.00	60.00	16.00	1.00
American Whites	Miller et al., '51	460	22.83	71.52	5.65	0.00

[1] Taken from Mourant, '54.

TABLE 14

Duffy system

Peoples	Number tested	Number and per cent of phenotypes				Gene frequencies		Sum of gene frequencies
		Fy(a+)		Fy(a−)				
		No.	%	No.	%	Fy^a	Fy^b	
Maya								
In Mexico								
Chol	15	11	73.33	4	26.67	0.4836	0.5164	1.0000
Itza Maya	67	59	88.06	8	11.94	0.6544	0.3456	1.0000
Lacandon	33	32	96.97	1	3.03	0.8259	0.1741	1.0000
Tzeltal	111	94	84.68	17	15.32	0.6087	0.3913	1.0000
Tzotzil	91	83	91.21	8	8.79	0.7035	0.2965	1.0000
In Guatemala								
Cakchiquel	9	9	100.00	0	0.00	1.0000	0.0000	1.0000
Mam	24	24	100.00	0	0.00	1.0000	0.0000	1.0000
Quiché Maya	203	183	90.15	20	9.85	0.6861	0.3139	1.0000
Total Maya	553	495	89.51	58	10.49	0.6762	0.3238	1.0000
Non Maya								
In Mexico								
Chiapaneca	41	37	90.24	4	9.76	0.6877	0.3123	1.0000
Mextizo	19	18	94.74	1	5.26	0.7706	0.2294	1.0000
Totonaca	45	43	95.56	2	4.44	0.7892	0.2108	1.0000
Zapoteca	141	126	89.36	15	10.64	0.6738	0.3262	1.0000
Total Non-Maya	246	224	91.06	22	8.94	0.7010	0.2990	1.0000

ɪwn positive and negative controls. The ɹlts of the tests are shown on table 14. ;ene frequencies for Fy^a varied greatly ging from 48.36% among 15 Chol to ı% among 9 Cakchiquel and 24 Mam lians. The percentage of gene frencies for 553 Maya, however, was 32% and for the 246 non-Maya a 10% value was found for the Fy^a gene. ɪse values are high when compared :he 40.74% reported for 205 English ıtbush and Mollison, '50) and the 14% for 300 Minnesota Whites (Mat- et al., '54).

'or Amerinds the reported gene frencies of Fy^a are usually high: 74.74% 235 Blood Indians (Chown and Lewis,), 86.36% for 161 Chippewa (Matson l., '54), 67.84% for 58 Diegueno (Panand Kallsen, '53); with the exception wo studies in Brazil where Pantin and queira ('52) have reported a complete : of the Fy^a gene in 73 Brazilian Inıs, the population thus being presum- homozygous for Fy^b. Junqueira and hart ('56) have found a value of '2% for the Fy^a gene in 55 Carajas ans in Brazil. These low findings of if confirmed and established with the anti-Fy^b may be very significant. Unuch tests have been done there will ren the question whether or not there resent in Indians the third Duffy gene found in Africans (Sanger et al., '55) ch does not cause a reaction with either -Fy^a or anti-Fy^b. Since the Fy gene aprs so far to be peculiar to Negroes, it ld be surprising if it were found among Indians tested in this study although may expect to find it among tribes hich Negro blood has been introduced, the Blackfeet (Matson, '33). A low frequency for Fy^a (13.98%) has also found for Negroes living in the ed States (Matson et al., '58).

ther peoples reported to have a high frequency for the Fy^a gene are: wegian Lapps (Allison et al., '52) .89%). Chinese (Miller et al., '51) .15%), Ainu-Japanese (Simmons et '53) (86.00%, Koreans (Matson et al., (99.50% and Asiatic Indians (Cutı and Mollison, '50) (73.04%).

The Kidd system

Two anti-Jk^a sera were used in testing for the Kidd (Jk^a) antigen. One of these antisera came from a sensitized group A donor and was processed at the Minneapolis War Memorial Blood Bank. It was not absorbed and was used for group A and O bloods. For checking doubtful reactions and for group B and AB bloods, a commercial anti-Jk^a serum was employed. Positive and negative controls were satisfactory with these antisera. Anti-Jk^b serum was not available at the time these tests were done and therefore the genotype frequencies shown on table 15 were computed on the basis of tests done with Jk^a antiserum only.

From the table it is apparent that there is no appreciable difference between the incidence of Jk^a in the Maya and non-Maya population tested. However, the Maya in Guatemala generally show a higher incidence of Jk^a (100% Jk^a for 9 Cakchiquel, 87.5% for 24 Mam and 88.18% for 203 Quiché Maya) than do the Maya in Mexico or the non-Maya groups.

The gene frequencies calculated from the incidence of the Jk(a+) phenotype vary little between the Maya and non-Maya showing 54.36% for the Maya and 50.00% for the non-Maya.

So far as we know there have been no other studies done on the incidence of the Kidd blood groups among Indians in Central or South America. The high incidence of Jk(a+) among the Maya in Guatemala is similar to values reported for Blackfeet (87.18%) and Blood Indians (Chown and Lewis, '53) (92.27%), for Africans (Ikin and Mourant, '52) (95.25%) and for American Negroes (Rosenfield et al., '53) (92.79%). The incidence of Jk(a+) phenotype and the corresponding gene Jk^a among the Maya and non-Maya Indians in Mexico is not very different from that reported for the English (Race et al., '51) (76.62% for Jk(a+) and 51.65% for gene Jk^a) and two reports (Allen et al., '51; Rosenfield et al., '53) for American Whites (77.25% and 76.72% for Jk(a+) and 52.30% and 51.75% respectively for the Jk^a gene. Chinese in New York on the other hand are reported (Rosenfield et al.,

TABLE 15

Kidd system

Peoples	Number tested	Number and per cent of phenotypes				Gene frequencies		Sum of gene frequencies
		Jk(a+)		Jk(a–)		Jk^a	Jk^b	
		No.	%	No.	%			
Maya								
In Mexico								
Chol	15	11	73.33	4	26.67	0.4836	0.5164	1.0000
Itza Maya	66	43	65.15	23	34.85	0.4097	0.5903	1.0000
Lacandon	33	21	63.64	12	36.36	0.3970	0.6030	1.0000
Tzeltal	111	84	75.68	27	24.32	0.5068	0.4932	1.0000
Tzotzil	91	69	75.82	22	24.18	0.5083	0.4917	1.0000
In Guatemala								
Cakchiquel	9	9	100.00	0	0.00	1.0000	0.0000	1.0000
Mam	24	21	87.50	3	12.50	0.6464	0.3536	1.0000
Quiché Maya	203	179	88.18	24	11.82	0.6562	0.3438	1.0000
Total Maya	552	437	79.17	115	20.83	0.5436	0.4564	1.0000
Non-Maya								
In Mexico								
Chiapaneca	36	26	72.22	10	27.78	0.4730	0.5270	1.0000
Mextizo	19	12	63.16	7	36.84	0.3930	0.6070	1.0000
Totonaca	45	35	77.78	10	22.22	0.5286	0.4714	1.0000
Zapoteca	132	101	76.52	31	23.48	0.5154	0.4846	1.0000
Total Non-Maya	232	174	75.00	58	25.00	0.5000	0.5000	1.0000

TABLE 16

Diego system

Peoples	Number tested	Number and per cent of phenotypes				Gene frequencies	
		Di(a+)		Di(a−)			
		No.	%	No.	%	Di^a	Di^b
Maya							
In Mexico							
Chol	15	4	26.67	11	73.33	0.1436	0.8564
Itza Maya	67	17	25.37	50	74.63	0.1361	0.8639
Lacandon	33	11	33.33	22	66.67	0.1835	0.8165
Tzeltal	111	11	9.91	100	90.09	0.0508	0.9492
Tzotzil	86	13	15.12	73	84.88	0.0787	0.9213
In Guatemala							
Cakchiquel	5	0	0.00	5	100.00	0.0000	1.0000
Quiché Maya	46	8	17.39	38	82.61	0.0911	0.9089
Total Maya	363	64	17.63	299	82.37	0.0924	0.9076
Non-Maya							
In Mexico							
Chiapaneca	41	3	7.32	38	92.68	0.0373	0.9627
Mextizo	19	4	21.05	15	78.95	0.1115	0.8885
Totonaca	43	9	20.93	34	79.07	0.1108	0.8892
Zapoteca	141	21	14.89	120	85.11	0.0775	0.9225
Total Non-Maya	244	37	15.16	207	84.84	0.0789	0.9211

'53) to have a low percentage incidence of the Jk(a+) phenotype (52.43%).

The Di^a antigen

Enough anti-Di^a serum was made available to us through the goodness of Drs. M. Layrisse, Banco de Sangre, Venezuela and B. Chown, Rh Laboratory, Winnipeg, Manitoba, Canada, to test 363 Maya and 244 non-Maya in this study. The antiserum was of excellent quality being specific and potent with known positive controls.

It is not known definitely at this time whether or not Di^a represents a new system. In table 16, however, the findings are recorded as positive or negative to anti-Di^a serum and genotypes are calculated on the assumption that there is a corresponding allele Di^b.

The table shows appreciable variation in the incidence of the Di^a antigen (from 0.00% in 5 Cakchiquel to 33.33% among 33 Lacandon, many of the latter being related. The percentage incidence of the phenotype Di(a+) for the 363 Maya is 17.63% and for the 244 non-Maya it is 15.16%. The per cent of genotype frequencies for the Di^a gene varies the same way (from 0.00% for the Cakchiquel to 18.35% for the Lacandon). However, the per cent genotype frequencies for total Maya and total non-Maya are closer together being 9.24% for the Maya and 7.89% for the non-Maya.

Other studies of the distribution of the Di^a antigen among Amerinds and other peoples have shown that Amerinds (Junqueira et al., '56; Layrisse and Arends, '56; Layrisse et al., '55; Lewis et al., '56), Chinese, Japanese (Layrisse and Arends, '56a) Koreans (Matson et al., '58), possess in varying distribution the Di^a antigen whereas Polynesians, Australian Aborigines, Papuans, New Britain natives (Simmons, '57), Eskimos (Lewis, Chown and Kaita, '56) and Caucasians (Levine et al., '56) do not have it. Since Polynesians (Nigg, '30 have a high percentage of A$_1$ and since the Blackfeet Indians (Matson, '33; Matson and Schrader, '33) also are preponderantly a group A$_1$ people, it would appear to be important to study the Blackfeet for the presence of the Di^a factor.

SUMMARY AND CONCLUSIONS

1. A study of the distribution of hereditary blood factors among 801 M and non-Maya Indians in Mexico Guatemala has been reported. Of th 553 were Maya including Chol, Itza M Lacandon, Tzeltal, Tzotzil, Cakchiq Mam and Quiché Maya and 248 non-M including Chiapaneca, Mextizo, Toto and Zapoteca.

2. These blood specimens were te for the following antigens: A, B, O, M S, He, Mi^a, P$_1$, C, D, E, c, e, V, K, Lu^a, Le^b, Fy^a, Jk^a and Di^a. The number te in each group and number and percen incidence of phenotypes and the calcul per cent of gene frequencies are prese in appropriate tables.

3. With the exception of the Chia eca, all showed an extremely high dence of group O ranging from 76.2 for the Zapoteca to 100% for the Cak quel. The Chiapaneca showed 65.85% group O which is low for general body of Indians. The Blackfeet related tribes are an exception having proximately 80% A$_1$.

4. The M antigen is high and th is low as is common to other Ameri However, the Chiapaneca show an u ually high gene frequency for the N g (35.37%) which is very high for Indi

5. The differences are not great tween the Maya and non-Maya with spect to MS and Ms but the NS is h compared to Ns among the Maya whe among the non-Maya there is a more e table distribution of these chromoso

6. No He antigen was found am 246 Amerinds tested. The gene respo ble of the Henshaw (He) phenotype pears to be rare if present at all in th peoples.

7. Among 714 bloods from group Indians tested for the presence of the antigen none was found.

8. There do not appear to be any standing differences in the distribu of P$_1$ antigen between Maya and non-M Indians, but it is somewhat lower than incidence reported for the Chippewa Blood Indians, and somewhat higher t the reported incidence for Brazilian Diegueno Indians.

In the Rh-Hr system the average
igs among the Indians of this study
ır to be in general agreement with
observed among other Indians and
from Whites in the same respects,
ı high cDE, a low incidence or ab-
of cDe and cde and the presence of
chromosomes. The Chol, Cakchi-
Mam and Chiapaneca showed excep-
to this generality.

All except one of the 801 speci-
tested lacked the V antigen. This
o be expected since the V gene has
found only with the chromosome
and cdef and these chromosomes
found to be rare in these Indians.

No Lu(a+) phenotype was found
y of the 173 Maya or 109 non-Maya
ns tested thus giving a frequency of
· for the Lu^b gene (homozygous Lu^b

Nearly all the Indians tested were
negative, presumably homozygous
no positive. No homozygous KK were
l. Three Kk bloods were observed in
Maya (two of these were brothers)
4 Kk were observed in the 248 non-
.

The Le(a+b−) group is rare
g these Indians. The Le(a−b+) was
ost common phenotype (77.40% for
laya and 69.80% for the non-Maya).
−b−) was the next most frequent
otype.

The average percentage of gene
encies for Fy^a is high among these
ns (67.62% for Maya, 70.10% for
Iaya). These values compare favor-
with those reported by others for
inds.

The average gene frequencies cal-
ed from the incidence of the Jk(a+)
otype vary little between Maya and
Iaya Indians (54.36% and 50.0%
ctively). These values are somewhat
than those reported for Indians in
h Columbia and Alberta.

The per cent of genotype frequen-
or the Di^a gene varies from 0.00%
e Cakchiquel to 18.35% for the La-
n. The values for the Maya and
Iaya, however, are closer together
9.11% and 7.89% respectively.
findings are in general agreement
others among Amerinds.

17. Further studies should be done on the distribution of the hereditary blood factors among Indians in Central and South America.

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Gown for Measuring Subcutaneous
sue in Females

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study of the amount and distribution
ıbcutaneous tissue in adolescent males
females is now under way at the
versity of Nebraska (Fry, '57). This
y uses the Harpenden caliper (Tan-
and Whitehouse, '55) for measuring
utaneous fat deposits of the upper
, lower arm, waist, back, and knee.
measurement of these locations in
escent girls is often complicated by
reluctance of the subjects to expose
ıselves in some of these areas. A gown
1) was designed to overcome these
culties.[1]

ıe gown consists of two pieces of cot-
cloth measuring 90 mm by 60 mm.
pieces are sewn together across one
ıe 60-mm ends, leaving a 40-mm gap in the center through which the subject places her head. In the front of the gown there is a horizontal slit 15 mm in length located 15 mm in from the right hand side of the subject and 45 mm from the top of the gown. A similar slit running in a vertical direction is located on the back of the gown, 18 mm in from the subject's right side and 18 mm from the top. Ties are placed on both sides at 20 and 60 mm from the top.

The horizontal slit in the front permits the measurement of subcutaneous tissue at the waist and waist circumference, and the vertical slit in the back allows the

[1] The gown was designed by Miss Marion Wright, a student in the Department of Anthropology, University of Nebraska.

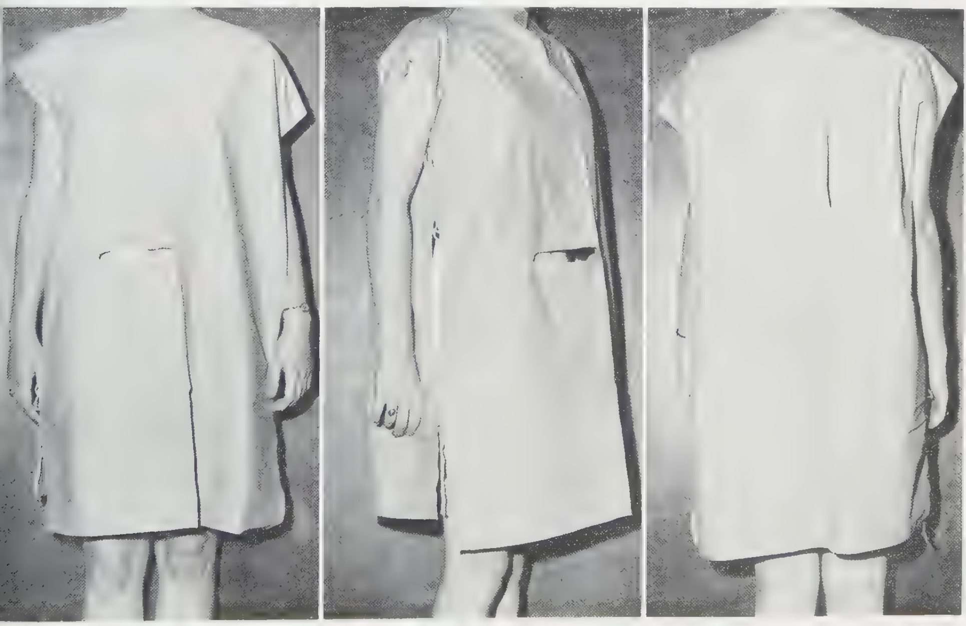

Figure 1

measurement of subcutaneous tissue on the back below the inferior angle of the right scapula. Since the gown is sleeveless, the tissue on the arms is easily measured, while the short length means that the knee is exposed when the subject sits.

Subjects of all weights and statures can be measured, since the gown fits loosely and the ties can be adjusted for girls of widely different circumferences. In addition, the use of the gown standardizes the measurement of weight, since all s[illegible] jects wear only the gown and their norr[illegible] underwear while being measured.

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e First Australopithecus Cranium from the Pink eccia at Makapansgat

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[r. R. S. Cunliff was in charge of the king party sorting the dumps at Makasgat for the final 4 months of field k in 1958. During December, 1958 srs. Alun R. Hughes and James W. hing were looking over blocks of bone-ing pink breccia when the latter spied block seen in these photographs and ght it away for development in Joaesburg.

gure 1 shows in the block the right al aspect of an australopithecine skull, of which has been wrenched away ng mining; it may be found somewhere ngst the 63 tons of breccia recovered ng that season. Below the skull whose tal region and face has been eroded y by natural weathering can be seen s of the broken second and third right ır teeth, the remainder of which must be in the block of breccia.

gure 2 shows the front or weather-ed aspect of the skull and the molar ı of both sides in frontal section. Off ıe right is another skull upside down eroded sagittally; apparently a speci- of *Parapapio broomi* the first cerco-ecid type to be found at Makapansgat. part of the dump is where *Cercopithe-es williamsi* was first found. It has proving so rich in cercopithecids since that it has generally been known ly as the "*Cercopithecoides* dump" un-ompletely sorted through and removed ng the 1958 season.

gure 3 displays the rear aspect of the alopithecine skull. The lambdoidal re- and the external occipital protuber- have been cleared sufficiently to in-e that this skull corresponds remark- closely with that of the female *Au-opithecus prometheus* first identified the occiput discovered by James ning in 1947.

Off to the left the lower jaw of the *Parapapio* skull can be seen. About halfway between the cercopithecid and australopithecine fragments lies the lower jaw of an infantile specimen probably of the same type of baboon (Freedman, '57).

No further development of the specimens in this unusual block will be done until casts have been prepared of the block in its present state and until a thorough search has been made amongst the aforesaid bone-bearing breccia recovered during 1958 for the missing slab of rock carrying the rest of the right side of the broken skull and its second and third molar teeth.

But whether that slab is found or not this block contains the most complete specimen of *Australopithecus prometheus* hitherto recovered at Makapansgat and corroborates the reconstruction made in 1948 and the inferences drawn therefrom.

The naturally eroded surface of the block displayed in figure 2 and the situation of the "*Cercopithecoides* dump"—at the crest of the dumping area on the hill slope just outside the quarries and between two mouths of the quarries—which the sorting party reached last year, now enable us to fix with tolerable certainty the position of this block in the original cave deposit.

This discovery and the original situation of this eroded surface block in the deposit have thrown further light on the deposit and have opened up hitherto unexpected prospects of further australopithecine finds in the pink breccia almost anywhere along the slopes of this amazing valley, so a few comments upon these matters are relevant.

The publication recently of the splendid detailed monograph on "The Transvaal ape-man-bearing cave deposits" by Dr. C. K. Brain ('58) enables anybody in-

Fig. 1 Cranium of *Australopithecus* seen from the right lateral aspect in a block of pink lime-consolidated (upper phase 1) bone breccia from Makapansgat Limeworks. The sectioned bone fragments above and below the skull have not been identified but the second and third upper molar teeth as well as the posterior part of the australopithecine maxilla are visible in section below the skull near the right margin of the block as seen from this aspect. Note the expanded parietal region of the skull just below the left thumb of the hands holding the block.

sted to localize the original position of block and the accompanying breccia he deposit with considerable precision. ighteen pages and 19 illustrations in Memoir are devoted to the Limeworks The "*Cercopithecoides* dump" lay ap- kimately midway between the two quarry mouths marked by the points H and X on Brain's figure 90 ('58).

From these points Brain drew his planes of section ABCD and XBFYZ through the deposit. They intersect at B on the surface of this pink breccia (upper phase 1 breccia of Brain). Just to the left of B, the point

Fig. 2 The upper or weather-eroded surface of the block of pink (upper phase 1) breccia displaying the coronally-sectioned australopithecine skull and its molar teeth on the left and the sagittally-sectioned baboon skull (*Cercopithecoides broomi*)—turned upside down—on the right. The criss-cross pattern on the block just above the australopithecine skull was made by the chisel of the developer. Some of the eroded and pink stained bone was also scratched with a scalpel the better to display the outlines of the sectioned skulls.

of intersection, Brain has shown the trench made by the limeworkers to remove the pink breccia that lay on top of the drip-stone or stalagmitic lime in the quarried area between B and the intersecting plane of section EF.

Brain's planes of section show that thickness of the stalagmitic deposit in particular part of the quarry was it greatest (up to 40 feet) and the overly phase 1 breccia eroded almost at its t nest (so that it formed a covering

Fig. 3 The inferior surface of the pink breccial block to display on the right the posterior or occipital aspect of the australopithecine skull. The lambdoidal region, the external occipital protuberance and the superior nuchal line on both sides have been partially exposed. At the left margin lies the broken lower jaw and cranium of the larger baboon. Between them and the australopithecine skull is the fragment of the lower jaw of a much smaller infant baboon (*Parapapio broomi*).

5–10 feet thick) over this great 40- thick deposit of stalagmite.

) it is patent why it was profitable for miners to make the trench through the mite at this point at an early stage in mining and to dump the pink (upper se 1) overlying breccia over the fairly oly falling hill slope nearby. The latter cleared of its "*Cercopithecoides* dump" last year and has yielded this precious .

rom the eroded face of the block dis- ing the two skulls in section it is ous that the australopithecine skull lain face upwards alongside these ba- fragments 5 to 10 feet from the ped part of the stalagmitic floor. Now the dripstone has been mined away underlying dolomitic hump, upon h it was deposited, is laid bare. Ob- ers (like Mrs. Alun R. Hughes in n's figure 92) naturally use it to sur- the cavern made by the miners when removed the dripstone. The ununatur- roof" of today's cavern made by the ers is formed chiefly by this unex- ted phase 1 (lower grey and upper) breccia, that formed the successive s of the cavern during australopithe- times.

ith one small, but most valuable ex- ion all the australopithecine frag- s discovered in the Makapansgat works dump during the past 12 years from the grey bone-rich *lower* phase eccia. That single exceptional frag- came from the most recent or phase eccia inside the quarry. It came from ace of the wall when the cone had col- d after the dripstone was removed, that part which contained the pebble identified by the late Professor C. Riet Lowe (Brain et al., '55).

e distinctive importance of this new alopithecine skull lies in its having deposited at least 5 feet above the gmitic floor and in the *upper* phase 1 ia lying between the grey breccia and tone-implement bearing phase 2 brec- The unexcavated part of this phase ccia is immense; it is exposed as an d land surface there today over an approximately 500 × 500 = 250,000 e feet.

From observations over the last two years we know that on the average 400 lbs of the lower phase 1 grey breccia occupies 9 cubic feet of space. The pink bone-breccia of the upper phase 1 breccia is more dense and probably on the average heavier. However, by applying the grey breccia weight to space formula to this 5–40 ft. thick unexcavated block of upper phase 1 breccia and assuming the average thickness to be 10 ft. the resultant 2,500,000 cubic foot figure shows that at least 50,000 tons of potentially autralopithecine-bearing grey, pink and reddish upper phase 1 breccia remains to be excavated at this site alone.

Any part of this surface and the underlying 5 to 40 feet of pink breccia (together with the 5 feet or more thickness of grey breccia below it) that still remains for excavation in the future may contain *Australopithecus* or contemporary faunal remains.

During 1958 we were able to keep our working party in the field for just over 9 months and were able to sort over 14,000 tons of dumped material and to recover some 60 tons of bone-bearing breccia principally of this pink type. The bone content of the pink (upper phase 1) breccia in general diminishes as one proceeds upwards in the deposit. This is due to two factors. First, the redness due to soil and wind-blown dust contamination increases with the enlargement of the cavern entrances. Secondly the greater the amount of entrant soil and dust the greater the acidity of the deposit and the less likelihood of bone preservation by the alkalinity of the lime-laden cavern moisture.

The 95 tons of bone-bearing breccia represents the fruits of the past 12 years' programme of dump sorting. Through the generosity of the Wenner-Gren Foundation and lately of the Wilkie Foundation this sorting has been carried right up the hillside to the quarries themselves.

The contemporaneity of *Australopithecus* with the entire period of cavern-filling deposition has been proven by australopithecine remains in each of its three characteristic types of breccia. But the point which I made last year (Dart, '58) and wish to emphasize again now is the relative triviality of the total 95 tons (35 grey, 60

pink) of breccia recovered from the dumps during the past 12 years as compared with the quantities previously removed by the limeworkers and the amount still remaining to be excavated.

I pointed out (op. cit., p. 929) that Eitzman ('58, p. 182) had observed three bone layers in the dripstone and had estimated that 300 tons of grey breccia were present in the middle layer alone. So the 35 tons of grey breccia collected from the dump (and of which we have developed only 7 tons so far) is merely a trivial sample of the total grey breccia deposit.

Similarly the 60 tons of pink bone-breccia collected from the dumps represents an infinitesimal portion of the pink breccia when compared with the 50,000 tons of unexcavated phase 1 breccia at this site. This unexcavated mass of phase 1 breccia still includes at its base, as is well known from numerous samples taken from the quarried cavern walls, a very considerable amount of basal grey and overlying pink bone-bearing breccia richly charged with bone, that may take a generation or two to remove.

Only when an extensive excavation been undertaken at Makapansgat, which this 10 years of dump-sorting gramme has served as an informative liminary, will we come to understand quately the life and habits of *Austra thecus* at Makapansgat. Meantime the velopment of the breccia recovered f the dump and the analysis of the os dontokeratic fragments it contains is y ing cumulative and highly rewarding formation.

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mments on the Photometric System[1]

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any of the technical aspects of the oMetriC camera have been aptly ed by Hunt and Giles ('56). An er study was made by Blesh, Meyers Kiphuth ('54). Most recently, the oMetriC system was used during the ner of 1957 in conjunction with an ropometric survey of more than 2000 in the United States Air Force. One e aims of the project, relating to the n of new equipment, was to ascertain anteroposterior and transverse di- ers are related to various body circum- ces. At each of the 6 air bases visited een 27 June and 31 August, the Pho- triC camera was installed. The field edure consisted of taking body circum- ces with standard steel tape and ing, with felt-tip pen, the anatomical s which would later serve as refer- on the projected photographic image. subject was photographed in both ing and seated positions. The posing ique of Dupertuis and Tanner ('50) generally followed for standing sub- I shall refer to 4 problems related is system of photogrammetry and in- possible solutions to them.

Hunt and Giles ('56) have called tion to the immobility of the Photo- C camera room. As one might ex- this difficulty can be minimized with y and muscle. In three hours, a team nen was able to dismantle, pack and all the camera room and other equip- which weighed approximately one nd was usually shipped by military ansport. To facilitate installation, a inverted U-shaped support (designed e PhotoMetriC engineer) was con- ed for the overhead mirror, thus ob- g the necessity at each air base for cial ceiling platform. As Hunt and have pointed out, distortion differen- aused by varying statures renders the ead view less satisfactory for anthropometric purposes. The metal support for the mirror reflecting this view, however, is necessary to secure the top pivot of the target (about the size of one of the mirrors and marked off in 6-inch squares) used for precisely positioning the mirrors of the camera room layout. The overhead mirror itself is useful in posing the subject.

2. Hunt and Giles ('56) considered the seated position "impracticable" to record with the PhotoMetriC camera. In the standard PhotoMetriC layout, this is certainly true. If certain modifications are made, however, the seated subject can be photographed—with exception of his toes. At our request, the PhotoMetriC Corporation made a test which revealed that the front mirror spanned 78.5 cm; the rear, 72.7 cm; the profile mirror, 80.6 cm. The latter, therefore, could potentially afford ample coverage for the buttock-knee lengths of air force personnel, which, according to the 1950 survey, have a mean of 60 cm and do not exceed 70 cm (Hertzberg, Daniels and Churchill, '54). Since the midline of the profile mirror in the standard PhotoMetriC camera room layout corresponds roughly with the center of the standing platform, the engineer moved the former along its conventional plane 9.6 cm away from the camera position in order to cover the buttock-knee lengths. This modification did not disturb the over-all relationships of the camera-mirror system, and provided the necessary viewing area in front of the seated subject.

The anteroposterior magnification balance, however, was affected. In order to accommodate all buttock-knee lengths, each seated subject was posed so that the midline of his torso was slightly be-

[1] This research was supported by the United States Air Force under Contract Nr. 33(616)–5246, monitored by Aero Medical Laboratory, Directorate of Research, Wright Air Development Center, Wright-Patterson Air Force Base, Ohio.

hind the point of zero magnification distortion. Thereby, the posterior plane of the torso was placed about 10 cm closer to the camera than it would have been in the standard standing position, while the anterior view was the same distance further away from the camera. Obviously, such a maneuver increased the magnification distortion of the rear view, while the front view, which was then approximately in the zero plane, had no appreciable magnification distortion. Problems of distortion in photogrammetry have been discussed by Tanner and Weiner ('49) and Gavan, Washburn and Lewis ('52). The former authors have mentioned the standard procedure for calculating magnification differences. The distance from the nodal point of the camera lens to the plane of operation is first determined. This figure, then, is divided by the over-all distance between the nodal point of the camera lens to the point of zero magnification distortion (9271 mm in the PhotoMetriC system. The quotient yields the percentage of the measurement of the photographic image which is represented by the real measurement. Therefore, in the PhotoMetriC system, the real counterpart of any measurement taken on a plane 10 cm towards the camera from the zero point is 98.92% of the magnified dimension. Thus, for every 10 cm closer to the camera, there is a magnification distortion of 1.08%.

Another approach to this problem is to include in the photograph itself a boldly calibrated scale at the plane where the measurements are to be made. All measurements taken at this plane can be directly gauged from the scale (Gavan, Washburn and Lewis, '52). For seated subjects we employed a "knee-plane marker" in this fashion.

A limitation to recording the seated view with the PhotoMetriC camera is that only the academically conventional left side can be photographed. On the standing view, the right side can be photographed by merely turning the subject 180 degrees. With the seated subject similarly rotated, however, the profile mirror would have to be shifted on its plane *towards* the camera position. If this is done, the focal paths of the mirrors cross one another.

3. Although the PhotoMetriC Cor[illegible] tion has apparently taken every precau[illegible] to make its mirrors distortion free ("c[illegible] ally flat within three thousandths o[illegible] inch tolerance" according to the comp[illegible] brochure), some contain minor distort[illegible] In the particular camera-mirror syster[illegible] used, the most disturbing distortion[illegible] curred in the front and side-view [illegible] rors. One meter from the floor, or app[illegible] imately from hip to waist level, the ce[illegible] 30 cm of the front-view mirror under[illegible] nified about 2%, while the same sectio[illegible] the side-view mirror showed approxim[illegible] similar distortion. Possibly distortio[illegible] the front and/or back-view mirrors [illegible] have contributed to the unreliabilit[illegible] measurements Hunt and Giles ('56) [illegible] sidered to be caused by "anteropost[illegible] sway of the body." Vertical dimens[illegible] reflected in the aforementioned area[illegible] these mirrors did not show underm[illegible] fication. In fact, there was a tendenc[illegible] the opposite direction. The rear-view [illegible] ror system tended to be relatively [illegible] with just a slight indication of overm[illegible] fication in some areas. The exigenci[illegible] rapid field installations and frequent t[illegible] port of the delicate mirrors may have [illegible] tributed to these slight inaccuracies[illegible] future installations, it might be worth[illegible] additional expense to test at least two[illegible] of mirrors to assure optimum results[illegible]

4. At the time of the Air Force's [illegible] anthropometric survey, the PhotoM[illegible] Corporation was using Eastman Kodak [illegible] X film, because its peculiar thickness [illegible] resiliency are best suited for the fri[illegible] film advance mechanism of the P[illegible] MetriC camera. The Eastman Kodak [illegible] pany ('58) rates this film's resolving p[illegible] as "medium" (76–90 lines per mm), [illegible] the enlargement potential is only "m[illegible] ate." Considering that the picture o[illegible] PhotoMetriC projection screen is hal[illegible] size, there is little wonder that image [illegible] nition leaves something to be desired [illegible] the future, different emulsions will [illegible] ably be available since the PhotoM[illegible] camera is being modified to accept st[illegible] ard 30.48 m rolls of 70 mm film inste[illegible] the specially rolled 5.5 m lengths form[illegible] used. Thus, other emulsions from A[illegible] Du Pont as well as from Eastman may [illegible] be employed if they possess the co[illegible]

ness and resiliency. The longer roll, entally, would have facilitated our ation when up to 130 subjects were ographed in one day.

is hoped that these few remarks will application in future use of the PhotriC system by anthropologists. In nary, the following comments about ystem can be noted: (1) it has been in extensive field work; (2) it can be fied to record the seated position with esults mentioned above; (3) the posty of slight mirror distortion should ken into account and minimized if ble, and (4) photographic emulsions gh resolving power would enhance the tiveness of the system.

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is project was initiated and carefully tored by 1/Lt. Frank P. Saul, USAF, e Aero Medical Laboratory's Anthroy Section, which is directed by Mr. E. Hertzberg. Mr. Theodore Yonkler, dent of the PhotoMetriC Corporation, most helpful in making arrangements low, for the first time, his delicate ment to undergo the rigors of a ner's field trip. Mr. Carlysle Richard, MetriC engineer, showed personal est in our problems and was largely nsible for the success of the USAF- Anthropometric Survey. The field was efficiently executed by men Gordon College under my direction. Messrs. Donald F. Booth and Norman T. Jeffries, Jr. performed most of the measuring on the PhotoMetriC screen, while the latter was also responsible for calculating magnification distortion. Mr. William H. Barton made substantial contributions to this study. We were fortunate to have Dr. C. W. Dupertuis personally inspect one of our field operations. Dr. Edward E. Hunt, Jr. has been gracious to read this paper and to offer valuable suggestions.

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Summary of Blood Group Phenotypes in Some Aboriginal Americans

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Phenotypes	Vicos Indians (Peru)[1]	Penobscot Indians (Maine)[2]	Athabascan Indians (Alaska)[3]	Tlingit Indians (Alaska)[3]	Eskimos (Alaska)
O	396	133	181	63	65
A_1	34	100	23	11	134
A_2	0	15	2	0	2
B	5	0	0	4	29
A_1B	0	1	0	1	11
A_2B	0	0	0	0	0
Rh_2rh	10	14	18	6	5
Rh_2Rh_2	95	12	73	37	62
Rh_1Rh_2	194	60	82	23	127
Rh_1Rh_1	114	58	17	7	43
Rh_1rh	15	83	8	3	4
Rh_zRh_2	2	0	4	2	0
Rh_zRh_1	5	0	3	0	0
rh	0	22	1	0	0
rh″rh	0	0	0	1	0
Rh_o	0	0	0	0	0
M, S−		36	109	42	121
	(M) 172				
M, S+		63	49	15	40
MN, S−		60	23	15	61
	(MN) 192				
MN, S+		60	24	7	16
N, S−		19	0	0	2
	(N) 64				
N, S+		11	1	0	1
Fy(a+)	319	196	205	79	236
Fy(a−)	28	53	1	0	5
Jk(a+)		201	153	62	170
Jk(a−)		48	53	17	71
P+	200	194	47	9	63
P−	228	55	129	21	167
Le(a−b+)	297	234	167	25	225
Le(a−b−)	95	6	9	4	5
Le(a+b−)	16	9	0	1	0
K+	0	1	1	1	0
K−	302	248	205	78	241
Kp(a+)	0	4	0	0	1
Kp(a−)	164	245	206	79	240
Lu(a+)	4	21	0	0	0
Lu(a−)	372	228	188	79	230
Di(a+)	74	20	1	0	2
Di(a−)	234	229	205	79	239

[1] Done in 1956; Allen and Newman.
[2] Done in 1958; Allen and Corcoran.
[3] Done in 1958; Corcoran, Allen, Allison and Blumberg

her Light on Australopithecine Humeral and
ıoral Weapons

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ı years ago I (Dart, '49) published in ɔurnal the first comparative study of ıboons from the South African man-eposits to display the predatory im-ntal technique of *Australopithecus* three sites. At that time the most ing evidence of his humeral bludgeon ique, apart from the double-vallecu-fractures in baboon skulls, were the r depressed fractures that spelled by murder for the two *Plesianthropus* ranial casts seen in figure 1.

: double-valleyed fractures were ob-y the work of double-ridged tools. Of the bone deposit at Makapansgat led generous evidence in antelope ri, whose distal ends — if not them-fractured — fitted easily into these ssions.

pite its clarity the evidence presented in illustrations and actual casts of nens was received with such doubt ne colleagues that we initiated a pro-at Makapansgat such as should exclude any reasonable doubt. We ɜded to extract all the available bone a from the dump and every bone ent from the breccia, however long ocedure might take.

he end of 1958 the entire dump area of the kilns and right up to the mouths had been sorted and 95 tons ne breccia recovered. This rather sive task, one that involved the sort-nd shifting of approximately 40,000 of rubble, could not have been ac-ished in that period without the ial help which came first from the er-Gren Foundation, and since 1955, he Wilkie Foundation.

nwhile only 7 tons of the gray a, of which 35 tons are available, been developed; but it has yielded 35,500 osteodontokeratic fragments or about 5,000 to the ton. But I had provided a preliminary statistical insight into its contents in the Memoir (Dart, '57a) on The osteodontokeratic culture of *Australopithecus prometheus* at a time when only 7,159 fragments were available. There I showed that distal ends of humeri were the most frequently found of all long bone fragments.

Incidentally, it became necessary to conduct collateral investigations, frequently distracting and involving considerable inconvenience, in order to confront traditional misconceptions with actual facts about the habits of rodents and carnivores *vis-à-vis* bone collecting (*vide* Dart, '56a,b, '57a, b, c, '58a, b) as compared with the bone collecting of human beings including the proto-human *Australopithecus*.

It is highly probable that, had these criticisms not arisen, the full import of the challenge presented by these ape-size-brained, but proto-human creatures at Makapansgat for understanding man's earliest known culture would have escaped notice. But it is important to recognize that one of the outstanding effects of the South African man-apes upon physical anthropology has been to display its limitations in assisting us to define what is man and what is ape anatomically. Makapansgat has meantime been exerting an effect of an entirely different sort. The absence of stones from the gray breccia there made it essential to search for australopithecine tools amongst the bones.

So physical anthropology had to enter a new phase. It had not neglected in the past physical defects due to human interference such as cranial deformation and trepanation, dental extraction and filing, and the like. Nor had it failed to include osseous changes in primates due to growth and disease as well as operative proced-

Fig. 1 Two *Plesianthropus* endocranial casts from Sterkfontein to demonstrate depresse fractures caused by double-ridged tools. The specimen on the left, seen from the rear, show a Y-shaped fracture running jaggedly from side to side across the midline in the pariet region. The elevated area between the two limbs of the Y shows the double-headed nature o the bludgeon used.

The specimen on the right, seen from the front, illustrates the accurate impact of a doubl ridged tool that smashed through the two parietals either side of the elevated midline; an forced the lower border of the right parietal (left side in picture) bone to slide down insid the squame of the temporal bone.

Fig. 2 Fifteen pairs of antelope humeral fragments from Kalkbank and Makapansga Limeworks (Kalkbank left, Makapansgat right in each pair). *Left side*: 5 pairs of dista ends at corresponding stages of destruction; *right*: 5 pairs of proximal end fragment *central part*: 5 pairs of distal ends to show the combination of pounder and spiral blade the generally formed and their usefulness as blades even when split longitudinally.

But Makapansgat caused physical)pologists to acquaint themselves also he rudiments of forensic medicine as s to acquire an expanding acquaint-with comparative anatomy in order vide evidence of man.

night be reasonable to argue that handiwork is the domain of the eologist rather than of the physical)pologist if it were not for the fact ne training of the cultural anthropol-nas veered in the direction of stones eology rather than of bones and com-ve anatomy. It seems more appropri-ierefore at the present juncture to ue bringing comparative anatomical of the sort included in this communi-: to a physical, rather than a cultural anthropological audience though they clearly belong to both.

Kalkbank and Makapansgat

I was enabled recently with the assistance of Dr. Revil J. Mason and James W. Kitching (Mason, '58) to place on record a description of the Kalkbank Middle Stone Age site and a detailed comparison of the Kalkbank long bones and flakes with those from the Makapansgat Limeworks australopithecine site.

For the convenience of those who may not have access to that significant comparative study I am including here the figure (fig. 2) used there to compare the states in which antelope humeri are found at Kalkbank about 15,000 years ago and at

Fig. 3 Sheep femora split by James W. Kitching spirally through contrariwise twisting of e two ends of the bone after the shafts had suffered an impact; the left specimen with the oint of a stone tool, the right specimen by striking it on the edge of a wooden table.

Makapansgat the better part of 1,000,000 years ago.

The fragments are arranged in corresponding pairs (Kalkbank on the left, Makapansgat on the right in each pair) to display the exactitude of the correspondences between the two cultures at these two sites with respect to the ungulate humeri.

The 5 pairs on the left are a series of distal ends in various stages of disintegration as a result of use as clubs. The 5 pairs on the right are a series of proximal ends of various sizes struck off during use as clubs or pounders.

Five pairs of distal extremities occupy the center of the figure. They illustrate how humeri of the largest type were as triple-purpose tools: pounders, rators and blades at both sites. The b shaft served as a perforating point blade according to the manner in wh was broken or trimmed. Blade tools also secured by splitting the bone lo dinally. Samples of blades are see either side of the central pair in th row.

The spiral blade and dagger poin

James Kitching and I had ascert during this investigation that hu flakes were also the most frequently o ring type of bone flake found at

Fig. 4 XIII from Breuil's "Bone and Antler Industry of Choukoutien" to demonstrate th correspondences in the treatment of ungulate humeri to produce both spiral and pointe shafts by *Sinanthropus* in China with that used by *Australopithecus* at Makapansgat and b sapient man at Kalkbank in South Africa.

ank and Makapansgat. But we were gnorant of the means whereby primi-apient man at Kalkbank 15,000 years ınd the still more primitive proto-*Australopithecus prometheus* about ,000 years ago at Makapansgat ob-l these spiral blades until one Sunday eserved the femur from the family's leg of mutton.

e following day he brought it to the ıtory, struck the shaft with the point stone implement and, holding each f the bone in a hand, twisted them in opposite directions. The beautiful ant spiral blades and the point of :t of the stone implement are clearly on the left side in figure 3.

wever, no stones whatever, other than inutive sliver of quartzite, have been ntered during the development of 7 tons of the Makapansgat gray bone a. So the next time his Sunday joint led James Kitching with a further imental opportunity he simply struck the shaft against the wooden edge of the table and twisted the bone ends contrariwise again with the spiral, and pointed results seen on the right side in the same figure.

From these two specimens it is patent that a simple, but intelligence-demanding technique of making spiral blades and stabbing tools from humeri or femora had been invented by *Australopithecus* and was being carried on nearly a million years later by Kalkbank man.

Reference to Breuil's ('39) "Bone and antler industry of the Choukoutien Sinanthropus site" shows that the same technique was followed in China in the Middle Pleistocene (fig. 4). Breuil and Zbyszewski ('47) illustrated unwittingly humeral blades made by the same technique in their revision of the mesolithic industries of Muge and Magos. They have also included there a picture of a distal end of a humerus identical with some of those from Makapansgat and Kalkbank.

Fig. 5 A mint specimen of a humeral dagger prepared by *Australopithecus prometheus* at akapansgat by spiral fracture and trimmed to a point by flaking. Inset the other side of e dagger point: the original spiral blade also slightly flaked.

The pointed and trimmed nature of these humeral shafts from Makapansgat as well as their splitting demonstrates that *Australopithecus* understood as thoroughly as Kalkbank sapient man how to choose his antelope — large, medium or small — for his osteodontokeratic purposes; and also how to maintain by flaking, if he did not achieve it by breaking, the sort of point or blade he needed.

Figure 5 has been chosen to illustrate this matter of dagger preparation by the man-ape. It presents a fossil antelope humerus from Makapansgat broken spirally and with its trimmed and pointed end lying on another bone, an ulna of an antelope. Inset in the same illustration is a photograph of the other side of this dagger point. Figure 6 gives the reader an opportunity of seeing this weapon as it lay in the breccia. Simultaneously it provides an unusual picture of finding objects of similar function stored together.

This tool-stacking feature of the
kapansgat man-ape deposit was
trated in the memoir on The
dontokeratic culture of *Australopit*
prometheus in respect of ant
skulls, palates and bone flakes.
demonstrated here in respect of da
because we find in this block, in ad
to the intentionally-fashioned humera
ger, natural antelope ulnar and g
horn-core daggers. To their left lie a
levering rib and a pounding or trim
calcaneus, or hock bone frozen togeth
they lay there, by the white lime drip

From the facts presented here
patent that the antelope humerus ow
prevalence at Makapansgat and its pe
ence at Kalkbank, as well as its disp
from South Africa to Peking in the
East and to Portugal in the north we
the fact that it was the most generall
viceable domestic appliance discover
Australopithecus. It seems to have

Fig. 6 An australopithecine example of stacking similar tools together. The three daggers gazelle horn-core, antelope ulna and pointed humeral shaft, lying upon one another an embedded in the dripstone with a levering rib and a calcaneal pounder to the left of th gazelle horn-core.

ncestor simultaneously of the kitchen and rolling pin, of the intentionally oned dagger as well as the club.

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ir from a Kadar Woman of India[1]

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n January 21, 1957 Dr. Carleton S. n cut a sample of hair (composed of oximately 100 hairs) from the head of ung woman, about 20 years old, in Kadar Camp at Ittianey, Kerala State, a. The sample and a photograph of young woman were sent to this depart-t for study and comparison with hair oles of known racial origins.

oon ('58) has stated that some of the rs are Negritos and others are Aus-id in appearance. It may be expected mixtures of the two, or of either with r inhabitants of India, will present of mixed characteristics.

the outset mention should be made e fact that hair from a series of indi-als of any given group shows a wide e of variation as do also individual s from a single individual. Thus, the ngs from the present sample could ely suggest the genetic constitution of ndividual from whom it came.

OBSERVATIONS

rm. The gross form of the hair was rmined according to Martin's classifi-n ('28). From the sample and the re of the donor the hair appears to eeply waved with the distal ends more . However, Coon, in his letter accom-ing the sample stated that most of the en in the camp used an oil to "dekink" hair and that this particular woman tried it unsuccessfully. Coon also d that the members of the camp who returning from a gathering expedi-had "kinky" hair.

lor. The hair was compared with the rfarbentafel" of Fischer and Saller) for color determination. It matches sample which is designated as Y, the est color on this scale, and is in the nblack range.

dex and area. The hairs from ap-imately half the sample were sectioned transversely with the J. I. Hardy thin cross-section device (Trotter and Duggins, '48) in order to determine the area and the shape or index of the cross-section. The index was determined by using the formula:

$$\frac{\text{least diameter} \times 100}{\text{greatest diameter}};$$

and the area by the formula:

$$\tfrac{1}{2} \text{ greatest diameter} \times \tfrac{1}{2} \text{ least diameter} \times 3.1416.$$

The greatest and least diameters were measured microscopically with an eye-piece micrometer and then converted into square millimeters from the area formula. The average index and area in mm^2 of the 50 hairs measured is: index—69.74; area —0.0050 mm^2. The range of indices is 54–95 with the greatest number in the 65–69 group; while the range of areas is 0.0026 mm^2–0.0072 mm^2 with about 50% between 0.0046 mm^2–0.0055 mm^2. It is not unusual to find a wide range of any one characteristic in hairs from any one person.

Medullation. Approximately 25 hairs from the sample were placed parallel on a slide, immersed in zylol, and the length of the shaft examined through low power of the microscope to determine the presence or absence of a medulla. The classification, absent, scanty, broken, and continuous (Wynkoop, '29) was used, and a record kept of the type in each hair. The results are:

Absent	68%
Fragmentary	32%
Discontinuous	0%
Continuous	0%

The hair being heavily pigmented made visibility of the medulla difficult and so an approximate check was taken by ex-

[1] This study was supported (in part) by a grant-in-aid from the Wenner-Gren Foundation for Anthropological Research, Inc.

amining the cross-sections for evidence of medulla. Such evidence was apparent in 17 of 57 hairs, which tends to substantiate the percentage of medullas found by the first method.

DISCUSSION

The area or size of the questioned sample, 0.0050 mm^2, (fig. 1) most closely approaches the size of average Mongoloid hair (0.0051 mm^2—based on a number of samples from Chinese, North and South American Indians, Eskimos and Thais) and is much larger than the average area of 22 Negroid groups studied to date in this department (fig. 2). These 22 groups include samples from Madagascar, Tasmania, Southern Rhodesia and New Guinea with an average size of 0.0032 mm^2. They range from 0.0019 mm^2 for the Keimoes of South Africa to 0.0048 mm^2 for the Antanosy of Madagascar.

Fig. 1 Cross-sections (× 220) of hairs from a Kadar of India.

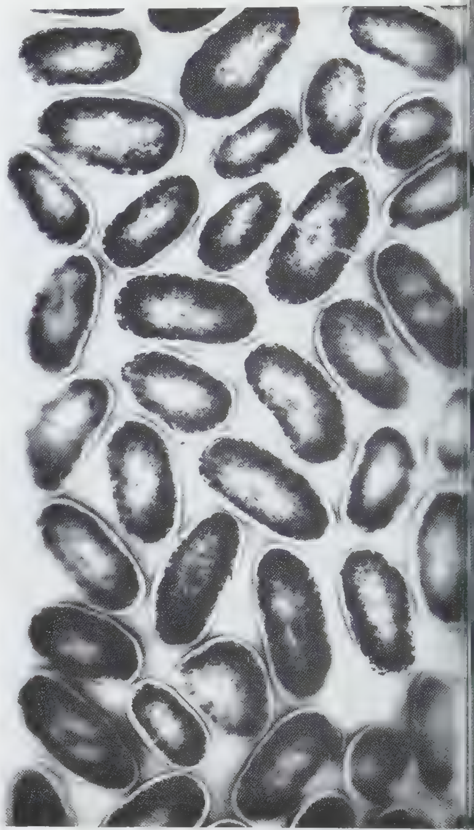


Fig. 2 Cross-sections (× 220) of hairs
a Zulu.

The average index of the Kadar san
of 69.7 falls between the average ind
of Negroid hair, 59.5, and, 80.9, for M
goloid hair. In fact it most closely appr
mates the 69.6 index for the hair of A
tralian Aborigines. However, in one of
Negroid groups, the Merina of Madagas
an average index of 71.0 was recorded

The low percentage of medullas (32
located in the Kadar hair again approac
the Negroid characteristic of few medu
as recorded for the Korana, Keimoes
Zulu (31%) and is much lower than
68% figure for Mongoloid hair.

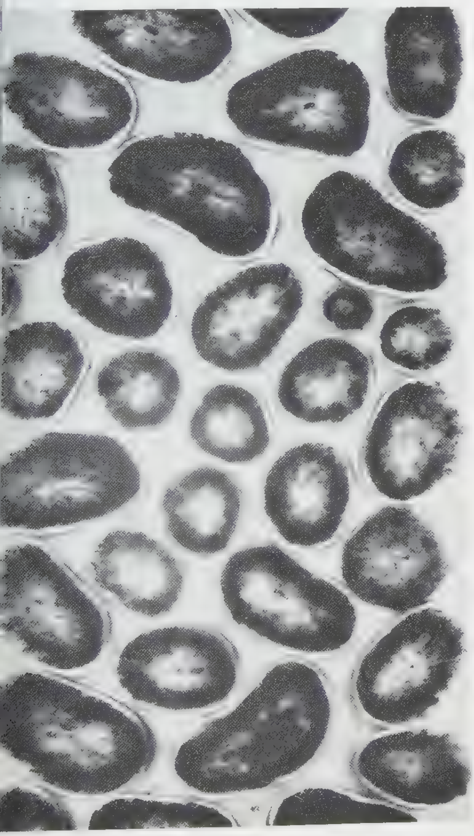
The hair form, "Curly to Kinky," rel
the Kadar specimen to this same charac
istic in Negroid hair while the hair co
"brownblack," falls within the color ra
of either Negroid or Mongoloid hair.

A search through the file of hair sp
mens revealed that the Kadar san

TABLE 1

Averages of characteristics of hair from samples of various racial sources

Source—collector	Area	Index	Medulla	No. of samples
	mm²		%	
Korano, Keimoes, Zulu—Gates	0.0025	53.20	31	34
Zulu—Stewart	0.0031	54.79	25	9
Zulu—Gates	0.0033	47.47		3
Arnhem Land—Setzler (Australia)	0.0032	70.90	35	197
American Negro—Trotter	0.0033	48.47	38	125
American White—Trotter	0.0033	73.74	36	163
Madagascar—Singer, Gates	0.0040	64.80	49	392
Hindu—Gates	0.0041	83.20		3
Yupa Indians—Gusinde	0.0045	85.00	67	26
¾ Hindu × ¼ Zulu—Gates	0.0049	70.00	24	1
Kadar—Coon	0.0050	69.70	32	1
India—Theophilas	0.0050	77.00	32	20
India—Graham	0.0052	74.00	49	21
Thai—Dhira	0.0052	81.80	54	68
Chinese Students—Trotter	0.0060	79.66	73	30



g. 3 Cross-sections (× 220) of hairs from individual of Natal, Africa, ¾ Hindu and Zulu.

rather closely resembles a single specimen submitted by Gates to this laboratory in 1956 as ¾ Hindu and ¼ Zulu (fig. 3). This sample was collected along with other pure Hindu and pure Zulu samples from Durban and Dundee, Natal, Africa.

The area, index and percentage of medullas recorded for hair samples from a number of racial and national groups are listed in table 1 together with those for the present sample.

CONCLUSION

As was pointed out earlier the wide range of characteristics within the hair of an individual makes it difficult to predict origin based upon hairs taken from just one subject. The average of measurements taken on samples from a larger group would be more indicative of race. Based upon measurements and examination of hair from the Kadar subject in question, it will be noted that the area of the specimen most closely approaches the average area for Mongoloid hair, while the low percentage of medullas is characteristic of Negroid hair. The index or shape of the specimen and its form fall between the Mongoloid and Negroid and the color falls within the range of both. It would therefore appear that some Negroid and some Mongoloid characteristics are represented in the specimen.

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APPENDIX

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The Kadar are a group of about 500 persons living in the Cardamon Hills of Cochin State, South India. Until disturbed by the march of progress, they were simple food gatherers who lived by digging roots in the forest, collecting a little slow game, and climbing trees and cliffs for honey. They did not touch the large animals with whom they shared the forest, and vice versa. These people have long been considered the nearest thing to a Negrito population in India, although certain Indian anthropologists have denied it. Actually they include both Negrito and Australoid phenotypes. Their preferred form of marriage in which ego marries his father's brother's daughter, may help to impede complete assimilation. This sample is from a woman of Negrito phenotype (fig 4). It is my observation that the hair of the Australoid phenotype is coarse. In Central India, among the Munda-speaking peoples, a Mongoloid element is present among the Australoid majority.

Fig. 4 Kadar woman of India.

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Relation of the Temporal Muscle to the m of the Coronoid Process[1]

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ne interdependence of bone and the ciated muscle has recently been re- ed at length by Scott ('57). As he cates, many lines of evidence show that ne post-natal development of the skele- areas for muscle attachment are de- lent for their normal expression upon functioning muscles which attach to n. This is particularly true of tuberos- and other bony prominences (Tower, Leriche, '39; Washburn, '47; Wolffson, Avis, '59). That some measure of elation exists seems certain. This fact e is of great utility to anthropologists wish to interpret the form of bone.

ne reasons for this dependence of bone n muscle are yet open to question. e attribute it largely to mechanical fac- e.g., tension exerted by the muscle on ving bone (Glucksman, '42; Washburn, . Others prefer to regard bone growth ne result of intrinsic factors whose ex- sion is made possible by the presence xtrinsic factors provided by the muscle, vascularization (Felts, '57).

he present experiment was designed to the mechanical situation, maintain- all other factors normal. This was omplished by removing a large amount he temporal muscle, leaving all that nediately adjacent to the coronoid cess. In this way it was hoped to sepa- the results of muscle tension from e of vascularity of the bone. To deter- e any concomitant changes in the in- al structure, the split-line method of ninghof ('25) was used.

MATERIALS AND METHODS

n a series of 10 6-week-old male cats superior portion of the right temporal scle was removed from the cranial vault severed just above the level of the omatic arch. The remaining portion of the muscle was not disturbed. The coro- noid process, surrounded by the residual muscle, was not exposed nor was it dam- aged in any way.[2] Recovery was rapid, and normal chewing of food was resumed as soon as the animals emerged from the anesthesia. The unoperated side of the jaw served as a control. The animals were raised in the author's home. Diet con- sisted of canned cat food, fresh kidney and liver, milk and, not infrequently, wild rabbits and birds. In the majority of the animals body growth was excellent. Con- tinual observation failed to disclose any preferential use of either side of the jaw.

The animals were sacrificed at the age of 16 months. All skulls were examined prior to maceration to determine the results of the operation. The bones were macer- ated by boiling for a short time in a 2% solution of acetic acid.

After the bones had dried a variety of measurements were taken to discover any differences which might exist between the operated and unoperated sides of the jaw.

Those mandibles which were to be used for split-line analysis were decalcified in a 5% solution of HCl until penetration by an ordinary sewing needle was possible. Following this, they were washed thoroughly in running water to inhibit further action of the acid. To rid the bone of excess moisture and localize the staining fluid, they were placed in an air-tight con- tainer for several hours. The punctures

[1] Work began under a grant from the National Science Foundation and continued with a grant from the Ford Foundation for the study of the Evolution of Behavior under the direction of S. L. Washburn. Successful completion of the project was largely owing to the efforts of Dr. William F. Irwin and Mrs. Fannie M. Avis, under whose care the experimental animals were raised.

[2] Surgery was performed by William F. Irwin, D.V.M., of Tulsa, Oklahoma.

were made and stained simultaneously by dipping the needle into India ink prior to piercing the bone. No attempt was made to draw out the splits into continuous lines in the manner of Pauwels ('50) and Tappen ('57) since the major alteration in the split-line pattern to be seen in the coronoid process on the operated side of the mandible was sufficiently demonstrated by the discontinuous splits.

For purposes of illustration the split-lines were redrawn on closely similar but undecalcified mandibles of the same series since good photographic reproduction of the original specimens was not possible

OBSERVATIONS

The operations were completely successful and had almost identical results. The temporal muscle on the operated side had not regenerated and extended only slightly above the tip of the coronoid process. The portion of the muscle which remained arose from the zygomatic arch and infratemporal fossa of the skull and inserted into the coronoid process.

Changes in the cranium following the operation were much like those seen earlier in the rat (Washburn, '47). At the dorsal border of the muscle lay the temporal line, bounding the infratemporal fossa, far below its position on the normal side. The parietal bone was reduced in thickness and lacked some of its normal curvature so that this aspect of the skull appeared flatter than did the opposite side. While the nuchal crest was well below normal in size, the interparietal bone had suffered an even greater reduction in growth.

Gross examination showed no abnormality of the dental arch and this impression was confirmed by the measurements taken after maceration. There was no differential wear of the teeth. The only difference between the two sides of the mandible lay in the coronoid process. The process on the unoperated side was similar to that of normal cats, but the coronoid process of the operated side, while only slightly smaller than its fellow, differed markedly from it in shape (fig. 1). In vertical dimensions the altered process was somewhat shorter than the normal one but the major change was seen to be the shift in its axis. Instead of describing a curve upward

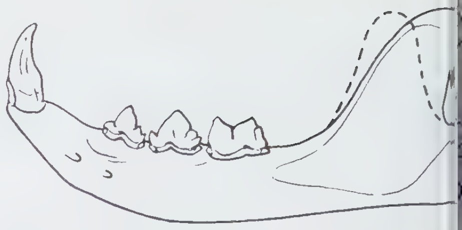


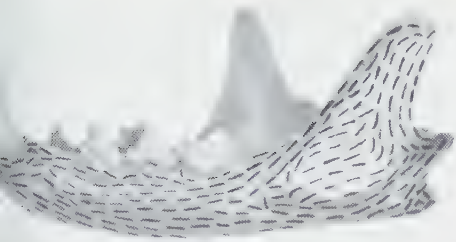
Fig. 1 Diagrammatic representation of th mandible showing the effects of partial rem of the temporal muscle early in the growth pe The outline of the operated side has been su imposed upon that of the normal side of the Solid lines, normal side; broken lines, oper side. (approx. nat. size)

and posteriorly as in the normal conditi the coronoid process of the operated of the jaw rose straight upward, lack entirely any suggestion of the nor curve.

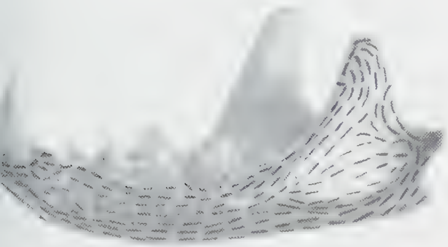
This modification in external form the coronoid process was also reflected the split-line pattern. On both of its faces a coronoid process is character by a pattern composed of two compone anterior and posterior. In the normal b these converge near the base of the proc and continue postero-dorsally in the cur axis of the bone, ending at its postero- sal border (fig. 2). In the altered coron process the posterior component greatly reduced in extent and the enlar anterior division deviated from its nor orientation halfway through its course become antero-dorsally directed and to adjacent to the antero-dorsal bor (fig. 3). This modification was even m marked in another operated mandible which the splits parallel to the ant dorsal border were absent and the ante component continued its course to the e of the bone (fig. 4). The remainder of mandible on the operated side showed departure from the normal split-line tern.

DISCUSSION

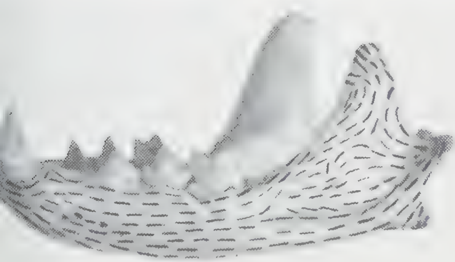
Removal of a large part of the tempo muscle, but not that surrounding the co noid process, results in a process not o somewhat smaller than normal but w an external conformation and inter structure notably deviant. Despite t the remainder of the mandible is co pletely normal in all respects, as shown figures 1–4.



;. 2 Normal side showing normal split-pattern.



;. 3 Operated side showing deviant pattern.



g. 4 Operated side in a different animal.

gures 2–4 Split-line pattern of the external ace of the cat mandible on normal and oper- sides of the jaw. The pattern of the internal ace of the coronoid process was closely simi-o that of the external surface. The patterns shown redrawn on undecalcified specimens of series. To facilitate comparison, the original side of the jaw is illustrated in figures 3 and 4 ne right side of the jaw. (approx. nat. size)

his circumstance supports the concept he mandible as a composite of rela-ly independent parts, a suggestion le by Washburn ('51) and elaborated Murphy ('57). Among an increasing nber of workers this concept, extended he rest of the body, has largely re-ed the older view whereby the body was regarded as a unit all parts of which had evolved in unison and a single feature of which might thereby serve as a valid index of taxonomic status. Thus Abbie ('51) speaks of the skull as "a mosaic of features which, within wide limits, can vary independently of one another" while Le Gros Clark ('55) voices the same belief in noting the need for the consideration of many characters, the "total morphological pattern," in any evaluation of fossil primate material.

But it is equally true, as much experimental evidence has shown, that an interrelationship does exist between certain of the features. It is also certain that such a series of interrelated features forms a pattern which underlies and makes possible the successful performance of a particular activity which forms an integral part of a way of life. Without experimental proof, identification of patterns and the interrelations of parts must rest on hypothesis alone.

The presence of another pattern in the mandible, embracing characters other than those here involved, has already been demonstrated (Avis, '59). In that case, as in the present one, changes in structure appear to be due to altered mechanical factors.

The removal of all the temporal muscle dorsal to the zygomatic arch effected two major changes. The strength of the muscle was reduced, and the direction of tension changed. Lack of abnormality in the dental arch together with the normal chewing pattern of the animals show that the muscle was a functioning one with adequate vascularity. Clinical work has shown that immobilization or non-use of any part of the body in the normal individual has as a consequence the partial or complete failure of osteoblasts (in the affected region) to secrete the organic intercellular substance which is calcified to form new bone (Albright and Reifenstein, '48). For this reason, the foregoing workers believe that "stress and strain stimulate osteoblastic activity." The smaller coronoid process in the present work is easily interpretable in terms of the lessened tension of the muscle and its effect upon osteogenesis.

External form is the visible result of osteoblastic activity expressed differen-

tially in a given region. It has been suggested that such a pattern of activity is intrinsic to a tissue and that vascularity is a major factor governing its expression (Felts, '57). But the pattern of vascularity in any peripheral area is highly variable in the individual (Ruth, '53). Granted that osteogenesis in an area is necessarily preceded or accompanied by vascularization, in the present case the pattern of vascular development has been modified from the normal one in apparent accordance with the newly acquired mean direction of tensile force exerted by the attached muscle. This is even more apparent if the split-lines indicate the mean orientation of the majority of the Haversian systems in the area, as they are belived to do (Seipel, '48). Regardless of the priority of either osteoblastic activity or vascular development, both have been similarly modified. It is concluded that tensile force (or its physiological effects) has altered the direction of tissue growth and that the modified coronoid process is an expression of this. Here the directive power of mechanical forces upon bone development seems clear.

Closely related is the change in the split-line pattern of the smaller coronoid process. Split-lines have been described as reflecting a variety of the constituent features of bone, the specific feature depending upon the type of tissue concerned (Seipel, '48), but each an important component of the internal structure. Whether the observed changes are produced by a "normal pattern of growth acting on a substrate of altered form" or by "mechanical adaptation" (Murray, '36), the fact remains that formation of the internal structure has shifted in conformity to the extrinsic forces acting upon it.

Results such as these lend support to Tappen's conclusion ('57) that those changes which occur in the split-line pattern of the juvenile gorilla skull in the transition to the adult condition are in response to altered mechanical conditions.

Recent developments not only make it possible to evaluate the morphogenic powers of muscle tissue but suggest the mechanisms by which many of the external prominences of cortical bone are, as Washburn ('47) suggested, maintained by their muscular attachments.

For example, in the mandible pric maturity, both outer and inner surface the shell of cortical bone enclosing medullary cavity (Breitner, '40; Weinm and Sicher, '55) are the scene of os genesis. Observations indicate the p ability that, as in long bones of rabbit rat (Brookes and Harrison, '57; Broo '58), arterial vessels of the medullary ity supply the nutrition for the cort bone. Clinical, experimental and deve mental evidence (Albright and Reifenst '48; Ruth, '53; Lacroix, '49) dem strate that resorption, most intense in th areas in most intimate contact with vascular system (Ruth, '53), proceeds ward from the medullary cavity and, lowed by appositional bone formation, models the basic circumferential lame deposited by the periosteum into the fa iar structure of Haversian systems. Ne section or non-use of muscle during period is followed by a greatly diminis rate of osteogenesis throughout the co in the affected region while loss of mu is accompanied by complete cessation bone formation, at least in the affec periosteal zone (Avis, '59). The nor rate of resorption on the inner cortical fi together with continuing osteoblastic ac ity in the surrounding normal areas of periosteum eventually engulfs the sta external region resulting in its disappe ance, as recent work coupling aliza staining with muscle removal has sho (Avis, '59).

In the adult, with the halt of os genesis in the periosteum at maturity, hibition of bone development through m cle loss or non-use is necessarily limi to the interior of the cortex (Allison a Brooks, '21) where remodeling contin throughout life in the normal individu Denervation experiments on the hume of the rat (Armstrong et al., '45) as w as clinical work on man (Albright a Reifenstein, '48) illustrate this. Reso tion continues at its normal rate and, si it is especially marked on the peripher of the medullary cavity, the latter croaches upon the cortical bone, reduc its radius (Allison and Brooks, '48). Wh the bone substance is thus decreasing volume its external dimensions apparen remain relatively stable (Ruth, '53) u

ge, with its failure of the peripheral ation (Bick, '55), introduces other rs.

seems clear from the foregoing sum- of recent work that no longer is there n to doubt the active role which me- cal forces, e.g., muscle tissue, play in aspects of skeletal morphology, that upon which so much stress has been d in phylogenetic studies. While it is less true that other processes are of derable importance in bone forma- recognition of bone-muscle relation- make it possible to place evolution- udies upon a much firmer basis than ofore. No longer is it necessary to e between hypotheses, of which there be a number, each equally logical. gnition of the activity patterns of these interrelated anatomical fea- are both the basis and the reflection d go far toward the solution of how came to be what he is.

SUMMARY

The superior portion of the temporal le was removed unilaterally in a series ung cats.

The coronoid process was reduced ly in size and its shape altered to a ed degree when the temporal muscle partially removed.

The split-line pattern of the coronoid ss exhibited striking changes after l removal of the temporal muscle.

The findings support the belief that andible is a composite structure made a number of relatively independent

The external form and internal struc- of the post-natal coronoid process are ly related to the functions of the oral muscle.

Some of the means by which muscle nces the external form of bone are ssed.

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ABO and Rh Blood Groups Among Chamorros of Guam

I REFERENCE TO ANTHROPOLOGIC AND GENETIC ꞌLEMS IN THE AREA

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: early investigations of the distribu- f the ABO blood groups in Micronesia been summarized by Boyd ('39). recently, Simmons ('52, '53), Gray- '53) and their associates in a series ɔers reported extensive data on almost the known blood groups among the ans, Trukese, Gilbertese and Kap- The purpose of this report is to ıt findings for the ABO and Rh blood s among 1,497 Chamorros on the . of Guam and to discuss their ɔpologic significance and possible re- ship to the occurrence of amyotrophic l sclerosis on the island. To our edge, this is the first report of the ɔution of blood groups among the orros.

ɑe background information about the . of Gaum and its people is in order. . is the largest of the Mariana Islands form one of the 6 Micronesian ɔelagoes. It has an area of 225 ə miles and lies 1,500 miles east of hilippines and 1,800 miles south of in the Western Pacific. The island iscovered by Magellan in 1521 but it ıot colonized by the Spanish until in the 17th century. When the first sh missionaries arrived in Guam in they were well received and were əd land for a mission by the local who were called *chamorri.* Later ɔanish applied the name to the whole : native population who came to be ı as Chamorros.

a result of wars with the Spanish erors, epidemics and famine, the ation of the Marianas, which was ated at 70,000 early in the 17th century, was reduced to about 1,600 in 1700. Many families from Guam escaped to the island of Rota, about 40 miles to the north of Guam, but a number of natives, mostly women and children, stayed on the island. The population then began to increase and, in spite of recurrent epidemics of smallpox and cholera, in 1855 the census showed 8,207 Guamanians. In 1856, a smallpox epidemic reduced the population to 4,724. Following this, the population increased steadily, especially after the occupation of the island by the United States in 1898, and by 1952 it was over 29,000.

Present-day Chamorros are supposed to be chiefly descendants of Spanish, Mexican and Filipino soldiers and the Chamorros who stayed on the island when the rest of the population fled to Rota. It is doubtful whether any pure-bred Chamorros exist today. A local school textbook records the death of the last pure-bred Chamorro as having occurred in 1826 (Searles, '37).

The present material was collected from blood donors at the Guam Memorial Hospital Blood Bank. By carefully reviewing the various data on the blood typing records, all "stateside" civil and military service personnel and probably 95%

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TABLE 1

ABO blood groups among the Chamorros

Number tested	Phenotypes per cent				Gene frequencies[1]		
	A	O	B	AB	r	p	
1,497	47.96	29.86	19.37	2.81	0.701	0.180	0.1

[1] Estimated using Bernstein's correction formulae (see Mourant, 1954).

of Filipino donors have been eliminated. The findings for the ABO groups and the estimated gene frequencies are given in table 1.

Of the 1,497 donors, only two were Rh negative (Rh typing was done for D only, using anti-D serum), and these were also of type O. This would give a gene frequency of 0.036. It was interesting, however, to find out that the two Rh negative individuals were a pair of male, presumably monozygotic twins whose family resides in Saipan. They deny any Carolinian, European or other admixture in their ancestry. The family has recently been investigated serologically by Dr. Robert S. Krooth to whom we are grateful for the above information.

COMMENT

A comparison of the ABO blood groups between the Chamorros and other peoples of Micronesia is given in table 2. It will be seen that the distribution of these groups among the Chamorros is similar to that among the Palauans, while it differs considerably from that among the Trukese, Gilbertese, and Kapingas. The greatest difference from the Palauans is in the O group, which is somewhat higher than in the Chamorros. The Trukese and Gilbertese are lower than the Chamorros in O but considerably higher in A and AB and only slightly higher in B. The Kapingas, although perhaps comparable in O, are considerably higher in A and lacking in B and AB in this small sample. With respect to the Rh factor, the Chamorros resemble the rest of the Micronesian and Pacific peoples among whom the Rh negative type is practically non-existent.

In his important article of the somatology and serology of Micronesia, Hunt ('50) views the area as a geographic unit and divides the peoples of Micronesia into three major groups: the Chamorros of the Marianas; the Trans-Micronesians who inhabit the area from Sorosol and T the southwest to the Marshalls and G in the east; and those who speak the nesian language in the southern Ca and Ellice Islands.

Simmons et al. ('52) consider the nesians to be a very mixed populatio deed, a large number of anthrop components have been ascribed to th various investigators, including Pc ian, Indonesian, Negroid, Mongoloid casoid, and recent Asiatic.

Simmons ('56) suggests that the h among the Gilbertese and Trukese co due to Polynesian influence and, sinc possibly a good Mongoloid marker, t usually high peak of B among th bertese may be due to Mongoloid influ It will be recalled that B is also high a the Chamorros although lower than a the Turkese and Gilbertese. It is p that there is Mongoloid influence a the Chamorros, too. Further anthrop evidence for this comes from Hunt who considers the Chamorros as met the most Mongoloid group in Micro Unfortunately, no further compariso be made at present because data o rest of the blood groups amon Chamorros are lacking. Such data ar becoming available for a smaller s of Chamorros and will be published

The more recent Spanish, Filipin Japanese influence among the Cham is also widely recognized, as men earlier. It seems, however, that the ture of Spanish blood among the Cha population has been given undue p nence and is certainly not borne out Rh findings, for the frequency of th negative gene among the present Spaniards is quite high, ranging fro to 40%, (Mourant, '54) while th negative type is almost absent amo Guamanians.

This is interesting in connection the hypothesis advanced by Kurland,

Comparison of the ABO blood groups in the Chamorros and other Micronesian peoples

Population	Investigators	Number tested	Phenotypes per cent				Gene frequencies		
			O	A	B	AB	r	p	q
Gilbertese	Simmons et al., 1953	150	12.6	44.0	28.9	14.5	0.340	0.382	0.278
Trukese	Simmons et al., 1953	117	23.1	40.2	22.2	14.5	0.486	0.319	0.195
Palauans	Simmons et al., 1953	191	56.5	23.6	16.8	3.1	0.753	0.143	0.104
Kapingas	Simmons et al., 1953	46	57.0	43.0	0	0	0.75	0.25	0
Chamorros	This study	1,497	47.96	29.86	19.37	2.81	0.701	0.180	0.119

'58), concerning the occurrence and frequency of amyotrophic lateral sclerosis (A.L.S.) among the Chamorros of Guam. It is now well-established that A.L.S. among the Chamorros is about 100 times more prevalent than in the United States and that a considerable number of cases have positive family histories, suggesting dominant inheritance. Kurland theorized that the A.L.S. gene may have been introduced by the Spanish and that it may have spread and been fixed to its present high frequency either by genetic drift or by balanced polymorphism.

In view of the almost complete absence of the Rh negative type among the Chamorros, it seems unlikely that any appreciable mixture of Spanish and Chamorro has taken place or that the A.L.S. gene has been introduced by the Spanish.

On the other hand, it is possible that the Rh index is not a reliable one. The absence of Rh negative individuals among the Micronesians and neighboring Pacific peoples may be due to the operation of some selective force which results in its elimination. If this be so, the same selective mechanism might tend to eliminate the Rh negative type from among the Chamorros, even if the gene had been repeatedly introduced by the Spanish. Unfortunately, at present, nothing is known about these selective values associated with the Rh negative gene. It is hoped that the genetic studies now conducted on Guam will help to clarify the significance of the high frequency of A.L.S. on the island and the relationship, if any, of the distribution of blood groups to the occurrence and frequency of A.L.S. there.

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e Chemical Analysis of Fossil Bone: ividual Variation

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umerous attempts have been made in ecent as well as the more distant past nd a relationship between the chem- constituents of a fossil bone and its able age. The student who has investi- l the history of these investigations undoubtedly have been impressed by act that although several components ssil bone tend to show a reduction letion) or increase (accumulation) age after burial the numerical data orting such trends have never given ence of that consistency, clarity and sion which is to be desired for an t system of dating. Several investi- s have remarked upon this circum- ce. For instance Thunberg ('47) on menting on the reduction of citric in fossil bone states his belief that nethod is not adapted to precise dating use of the irregularity of the data. ey ('51), in his review of the fluorine g method, published in the Viking l Year Book for 1949, says regarding work of Carnot (1893), "If one ex- es Carnot's individual analyses it be- s evident however that the averaging ures the important fact that there is de variation in the fluorine content nes of the same geological age from rent localities."

spite of the quite general dissatisfac- with results of analysis by chemical ods no systematic attempt has yet made to assess the factor of indi- l variation as such and to evaluate an obstacle to the success of the edure in determining the age of arch- gical specimens. This gap in our ing is the more surprising in view of reat care with which anthropologists subjected the physical measurement eletal material to searching statistical sis. It seems therefore worthwhile to call this matter to the attention of archae- ologists and other interested students and to point out at the same time some of the subsidiary problems involved.

Much of the work in the past has in- volved the analysis of single bones; rarely has there been any effort to establish the measure of a component through a series of similar examples. For example, Carnot based his fluorine comparisons (as well as those of phosphorus, calcium, iron and carbonate) upon a series of modern bones consisting of three human specimens and single specimens, one each from 16 dif- ferent animals. He therefore took account of variability in neither different bones from the same species nor possible inter- specific variation. With his fossil bones he consistently followed the same procedure by analyzing single bones from different animals and from scattered localities. Thunberg ('47) used no more than two samples each from three humans and three animals, all derived from varying localities and times. Pin ('50) analyzed for numer- ous components in but 4 human bones representing three diverse archaeological periods: "Recent," "Grimaldi" and "Pres- les." Gangl ('39) analyzing for fat, used one beef bone and 4 human bones, each of different age and provenience. Jaffe and Sherwood ('51) give values for uranium, fluoride, and phosphate from 10 fossil manatee ribs, two fossil shark teeth and one recent manatee rib. The manatee ribs were regarded as being of widely different ages. Barber ('39) analyzed for calcium, phosphate, carbonate, and nitrogen in 25 bones which were from different localities and ranged in time from "alluvial" to the Oligocene. Oakley ('51), on the other hand has used considerable care and has checked his critical specimens (such as Galley Hill and Piltdown) with control series of from

4 to 10 animal bone samples taken from the same localities and horizons where these human skeletons were found.

If uncontrolled individual variation between bones is of significant magnitude then it is evident that the analytical result obtained with a single sample is subject to possible serious error, and if so, then much of the older work, beyond establishing very broad trends, is subject to great reservation. It is desirable therefore to examine to what extent individual variation exists in series of comparable chemical or physical analyses.

It will be permissible to utilize the bone series analyzed in the Departments of Physiology and Anthropology at the University of California (Berkeley) since these are the most extensive with which we are familiar.[1] Numerous components have been tested, but those selected for discussion here are nitrogen, carbon and water. We have analyzed over 600 samples, results for 455 of which are given in table 1 and 168 in table 2. Our procedure has been to secure as many bone samples from each site, or locus of deposit as possible, in order to obtain the best average we could for each site. Hence the variability of individual bones within each of a number of fairly homogenous series can be estimated. In the tables are shown the number of samples analyzed from each site and the mean values for carbon, nitrogen and water, expressed as per cent by weight of the bone. Variation is measured by the standard deviation. However since the means differ widely in absolute value, the standard deviations have been converted into percentages of the corresponding means, i.e., the coefficients of variation. It will be observed at first glance that the coefficients of our series range from 3.1 to 75.1% of the corresponding mean. Thus a relatively high degree of variability is indicated.[2]

Before discussing the possible causes of variability two preliminary points must be considered, viz., the distribution curve and the sample number.

When skeletons are disinterred from a site customarily the exigencies of a small scale archaeology permit only a few to be recovered and these more or less at random. Hence the series which is available for chemical study represents only a dom selection from the total populat skeletons. One would wish to know, fore, whether the analytical values fo nitrogen or fluoride show the same bution around the mean as would be if a much larger group of bones, f stance 1,000, could be tested. But in tice it is impossible to secure and an any such enormous series and thus di discover the distribution. Consequent are forced to arrive at and rely upon reasonable assumption.

For orientation we may adopt a simple procedure, using for the pu our data for carbon and water. For of those sites where the carbon conte the bone lies between 2 and 7% by w and the water content lies between 5 7% we may recalculate the indiv experimental values of carbon and as per cent of the mean value for th involved. This puts all the values o same relative numerical basis.

Figure 1 shows the frequency dist tions for water in 225 bones and carb 421 bones. There curves appear t skewed very slightly to the left but o wise they take the form of normal dist tions. We cannot insist that the b

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[1] Previous publications pertaining to the in gation carried on in these departments w found in the biblography, under the nam the authors of this paper.

Numerous archaeologists have aided us b plying series of bone samples. Among thes Phil C. Orr (Santa Barbara Museum of N History), Harold S. Gladwin (Santa Barb W. A. Ritchie (New York State Museum), Cl E. Snow (University of Kentucky) and Stewart and M. Newman (U. S. National seum). To each of these we express appreci

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[2] It is of interest to compare the data giv table 1 with comparable figures cited by O for fluoride. Thus Oakley ('51) in his review fluoride values for 12 bone samples in the series of the Swanscombe group (table 3), si values for 12 samples in the pilot series o Ebbsfleet group (table 8) and values for 7 ples of the skeleton of Eoanthropus I (tabl The corresponding standard deviations and s ard errors, expressed as per cent of the m are respectively, for standard deviations 4.55, and 21.8. The same order of variation thus been found by Oakley as by us.

TABLE 1

Nitrogen, organic carbon, and water in fossil bones from 24 California sites

For each substance is shown the mean in terms of per cent by weight of the bone, the andard deviation expressed in terms of per cent of the mean (coefficient of variation).

Site	No. of samples	Carbon		Nitrogen		Water	
		Mean	C.V.[1]	Mean	C.V.[1]	Mean	C.V.[1]
ıte horizon group							
Co-138	20	5.82	33.7	2.35	46.4	7.03	12.2
ıc-6	24	3.76	42.8	1.47	58.7	5.49	30.2
arin County sites[2]	13	4.68	17.9	1.32	23.2	5.58	12.8
ıalwaj[3]	9	4.11	50.4	2.51	57.0	6.32	18.8
ecolote[3]	6	3.18	50.6	2.10	67.1	6.45	21.5
ısLLages[3]	13	3.63	26.4	2.41	31.2	6.56	17.3
ınta Rosa Island[3]	14	5.87	14.0	3.88	4.4	7.58	5.1
ın Miguel Island[3]	7 —	5.57	29.9	3.56	34.8	7.09	13.1
ınta Cruz Island[3]	6	6.30	7.1	3.82	6.8	7.88	3.1
iddle horizon group							
ıc-21	26	5.61	20.3	2.37	21.8	6.20	11.9
CO-141	18	7.86	21.7	3.66	13.9	7.23	8.7
ıc-43	30	4.05	30.1	2.04	32.8	5.96	12.1
ıc-151	33	2.73	41.0	1.15	57.0	4.34	18.1
ıc-104	9	1.52	36.8	0.64	40.2	5.51	18.0
Co-137	8	2.64	27.6	1.70	32.1	5.74	8.9
ıl-18	10	6.33	33.6	3.33	15.2	7.95	5.9
arin County sites[2]	10	4.35	20.0	1.04	28.9	5.41	14.7
arly horizon group							
Io-68	30	1.95	53.8	1.32	55.0	5.84	23.0
Io-142	31	1.09	75.1	0.54	53.3	4.30	14.9
ıc-107	32	1.59	35.6	0.44	67.9	4.28	15.1
Io-56	33	4.09	25.9	1.62	42.0	5.24	17.3
e-48	5	1.55	30.4	0.08	31.3	2.26	15.8
An-1	22	1.32	36.3	0.42	69.5	4.30	21.2
3a-7	10	2.64	21.5	0.70	46.0	5.83	12.2
ecial series							
ıc-6, single skeleton							
long bones	12	—	—	1.47	49.6	—	—
short bones	18	—	—	2.54	34.6	—	—
esh beef femur	6	5.72	8.26	4.01	3.69	11.10	3.58

[1] Plus and minus signs are omitted from the figures for coefficient of variation.

[2] Marin County sites: Late horizon group were Mrn-232b, -242, -266, -271 and -275. Those the Middle horizon group were Mrn-232b, -242, and -266. For archaeology of these see eardsley ('48).

[3] Of these 6 sites, all from the Santa Barbara area, the first three are described by Rogers 29); the unspecified island sites are some in which Orr has recently excavated but has ot described except in a general way (Orr, '51).

each site considered separately show lentical pattern but we can suggest here is no specific abnormal distribu- vhich repeats itself through many or the sites, for if there were such its nce should manifest itself clearly in omposite plot including 25 sites. It therefore be concluded that the or- components of fossil bone follow a antially normal distribution.

e problem of sample number is always lesome to the archaeologist. In our investigations we have invariably attempted to secure as many samples in each series and from each site as possible. Yet our numbers run only from 5 to 33. The standard deviations computed from our means for the three components under consideration indicate that even the upper limit of this range is too low for as accurate work as would be desirable. On the other hand to reduce the present average variability no more than half we would have to analyze 4 times the number of

TABLE 2

Nitrogen, organic carbon and water in fossil bone from 4 southwestern and three New York sites

Data formulated as in table 1. The southwestern sites, according to tree ring datin range from approximately 500 to 1,300 years before the present. For the New York materi the sites are allocated according to cultural criteria to the following periods: Wadswort farm, prehistoric Iroquois; Sackett, Owasco culture (immediately prior to Iroquois Frontenac Island, Archaic. The Kentucky material consists of a series of 27 samples fro various sites, all from the Adena cultural period and a series of 29 samples from th Indian Knoll site, of the Archaic period.

Site	No. of samples	Carbon		Nitrogen		Water	
		Mean	C.V.	Mean	C.V.	Mean	C.V.
Southwestern group							
Soda Canyon	10	—	—	4.35	3.51	7.55	2.7
White Mound	16	—	—	3.95	14.0	7.31	4.2
Hawikuh	37	—	—	4.33	7.1	—	—
Elden Pueblo	19	—	—	2.99	39.8	—	—
New York group							
Wadsworth Farm	10	2.58	21.2	1.27	32.0	6.48	10.0
Sackett	10	3.70	36.1	1.69	59.8	5.94	18.1
Frontenac Island	10	2.66	23.0	1.37	29.4	6.16	6.6
Kentucky group							
Various (Adena)	27	5.04	28.1	3.01	41.0	7.47	23.6
Indian Knoll	29	2.47	31.1	1.24	24.0	4.87	10.3

samples from each site, a task quite beyond the bounds of practicality not only for us but probably for most other investigators as well. We are thus obliged to fall back to the position of taking the data as they stand.

In view of these circumstances it is evident that a sharp limit is placed upon the precision with which any particular site may be dated. To come within one year or decade is out of the question. To specify a century, even with relatively recent material would be pushing the data

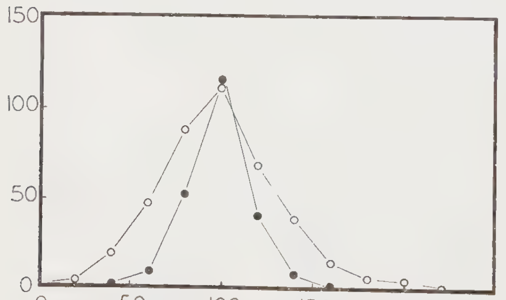

Fig. 1 Frequency distribution of carbon and water. Solid dots represent carbon and circles represent water. The ordinate is the number of cases and the abscissa the analytical values for the two components, referred to 100 as the mean.

to their extreme. Actually a time r should be established, representing limits of reasonable probability. Ev range of this type would have to b cepted provisional to the small numb samples necessarily available.

The variability of the chemical co uents of fossil bone can be traced prin to 4 sources: (1) experimental error i sense of unavoidable fluctuations in lytical procedure: (2) intrinsic differ between bones of a given skeleton; (3 ferences between analogous bones series of skeletons in the same site d physical and chemical fluctuations i soil matrix; (4) differences due to graphical location of the site. These siderations are discussed below. treatment must be verbal for the fa involved do not lend themselves t analysis of variance.

1. If the analyses for any of the mon bone constituents are properly ried out, whether by macro- or m methods, the standard error of esti due to this source alone should not ex plus or minus one or two %. This s to be the order of accuracy attaine Oakley, although he does not discus point specifically. For our own work

[cu]t of experimental error can be evalu[ated] from the special series on fresh beef (see table 1). We selected a piece [of] the central shaft of a fresh beef [femu]r, ground it and passed it through a [m]esh screen. The powdered bone was throughly mixed, thus eliminating [l]ocal variation in the bone itself. Six [para]llel samples were then analyzed by our [usua]l methods for carbon, nitrogen and [wate]r. The coefficient of variation for car[bon] was 8.26% of the mean value for car[bon], for nitrogen 3.69 and for water 3.58. [Sinc]e the carbon determinations involved [two] procedures (expulsion of carbonate with acid, and wet combustion with [chro]muric acid) the error obtained repre[sent]s the sum of the errors of the two [cont]ributory processes. The sample num[ber] (6) was very small. With a larger num[ber t]he experimental error would have been [corr]espondingly reduced. In any case the [vari]ation introduced by procedural tech[niqu]e is very much smaller than that in[here]nt in the bone itself.

In the initial phases of this investi[gati]on we made an intensive study of bones [from] a single midden, Sac-6, which we re[gard]ed as typical of the recent, or Late [Cult]ure horizon in the Central Valley of [Cali]fornia. We first took a skeleton at ran[dom] in its entirely and subdivided the [bone]s according to the anatomical nature, [segr]egating 12 bones from the legs and [arm]s. From each of these we took a seg[men]t from the middle of the shaft which [was] solid and compact. We then selected [12 s]hort bones (fragments of skull, verte[brae], pelvis, etc.) which were highly spongy [and] cancellous. Analyses were made of [seve]ral components, including nitrogen but [unfo]rtunately not including carbon and [wat]er. The nitrogen analyses however [wer]e themselves instructive. The mean [valu]e for nitrogen in the long bones [...]% by weight and in the short bones [...]%. The respective standard deviations [wer]e 49.6 and 34.6% of the corresponding [mea]ns. Using the standard errors as com[pute]d from the direct values of the means [the] Critical Ratio of the means (Fischer's [t va]lue) was found to be approximately [...] which for the sample numbers involved [is d]ecidedly significant. Subsequently we [sele]cted the central shaft portions of another 24 femora (from 24 skeletons) disinterred from site Sac-6 and found that their mean nitrogen content was 1.47% of the bone weight with a standard deviation of 58.7% of the mean.

This test clearly brought out two points. In the first place there is a wide disparity between long (compact) and short (cancellous) bone with respect to its organic content. This result has been obtained in essence by us many times and there can be no doubt of its validity. It is furthemore supported by the recent work of Graf ('49) who subjected fossil bones to very careful histological examination and found several types of cells still intact. Since the spongy bone contains in life far more blood and other living tissue than does compact bone it is not surprising that the organic content of the former, in the fossil condition, should run markedly higher than that of the latter.

For this reason it is important that chemical analyses be performed with a uniform type of bone, or at least that the bone analyzed be specified with reasonable anatomical precision. Since the long, compact bony structure is probably the more stable chemically we have invariably used it in preference to any other.

3. The variation between femora from different skeletons scattered through a site, as shown in table 1, is of the same order of magnitude as between the different bones of the same histological structure within a single skeleton. After death the bones are subject only to the influence brought to bear by the medium in which they lie, the soil of the site matrix. Throughout any soil mass, whatever its gross composition and texture, there are certain to be variations in particle size, moisture content, temperature and chemical composition in both vertical and horizontal directions. This condition of local disuniformity is particularly likely to arise in a habitation site which is formed from the most diverse materials and is the result of trash accumulation over a long period of time. Hence the chemical composition of a series of fossil bones, whether or not they are derived from the same skeleton, will tend to be altered quantitatively in varying degrees from point to point in

the site.[3] These local soil differences are random in occurrence, or at least are unknown to and uncontrollable by the investigator. Hence, as far as we can perceive at present, they cannot be avoided or predicted in advance in any analysis of chemical bone constituents. From this source, then, appears to stem much of the variability observed in a series of bones taken from the same archaeological site.

4. The degree of variability of a series of bones taken from within a single site appears to be somewhat different depending upon certain broad factors. Among these is the geographical location of the site. In order to illustrate this point we may classify our sites according to the geographical province in which they lie. We may then compare the average standard deviations, or coefficients of variation, shown by the bones within each subdivision. Such a test is not particularly rigorous but is adequate to bring to light any basic trends. The results are shown in table 3.

There seems to be no significant difference between those California sites which lie respectively in the northern and southern sections of the state. Moreover, the averages for three New York and two Kentucky sites (nitrogen determinations for the latter are not yet completed) appear to fall within the range encompassed by those in California. On the other hand the material from the arid Southwest (Arizona and New Mexico) gives evidence of more internal uniformity than that from either the Atlantic or the Pacific coastal belt. If this distinction is valid then it is quite probable that large-scale climatic factors are responsible. In the hotter dryer sites of the Southwest there is m less opportunity for the ground wat dissolve and transport organic and mi substance than in the moderately h coastal areas and Ohio Valley. We m therefore tentatively advance the prin that the highest stability among f bones is to be expected in regions of humidity and rainfall.

CONCLUSIONS

An extensive series of analyses for organic constituents (combustible car nitrogen and water) of fossil bones made possible the following conclusi

1. For a series of fossil bones fro specific site these constituents tend t normally distributed around the mea

2. The sample number of compar bones subjected to a specific type of a ysis should be as large as posible. N should the value for a single specime taken as definitive.

3. The variation of single bones, pressed as the standard deviation or as coefficient of variation is very great.

[3] We considered the possibility that, par larly in recent sites, the individual skeletons m vary with respect to the time during which had been underground and hence with re to the degree of fossilization. In order to test possibility we secured the records of *dept burial* for approximately 170 skeletons from a dozen sites. We attempted to correlate burial depth within individual sites as an i to duration of interment, with the chem composition of the bones. It is unnecessar cite detailed data because there was no appa correlation between the two factors. If such a relation does actually exist it is completely ridden by variations derived from other sou

TABLE 3

Average coefficients of variation for carbon, nitrogen and water, according to locality

Locality	Carbon	Nitrogen	Water
California			
Central Valley and northern coast (16 sites, 332 samples)	27.5	30.0	16.4
Santa Barbara Channel (8 sites, 87 samples)	29.7	33.5	13.1
Southwestern United States (4 sites, 82 samples)	—	16.1	3.5
New York State (3 sites, 30 samples)	26.8	40.4	11.6
Kentucky (2 sites, 56 samples)	29.6	31.5	16.9

cient of variation for a given group of : from the same site may range from nearly 100, depending upon the size e sample.

Variability is due in very minor part ocedural or experimental error. It is ible primarily to local fluctuations in hysical and chemical characteristics soil immediately adjacent to the indil bone.

Variability may be conditioned to extent by the general climate surling the site, particularly whether it or humid.

Individual variation constitutes a serobstacle to the successful establishof a precise dating system based chemical analyses for any fossil bone ituents.

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urrence of the Carabelli Trait in thwest Ethnic Groups

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1842 Georg von Carabelli, an Aus- dentist, described a tubercle present onally on the mesiolingual surface of ermanent maxillary molars, particu- on the first. Since that time it has known variously as *Tuberculum* Cara- *Tuberculum anomale*, or Carabelli's The many studies that have been hed on the subject in the past 115 have been concerned primarily with escriptive morphology, (2) its occur- in populations, (3) developmental my, and (4) mode of inheritance. has been no agreement on any one se 4 approaches.

ere is general lack of concurrence re- ng morphological features that may bsumed under the category of Cara- trait. This has produced an effective cle to the study of its distribution, de- ment, and possibly the mode of in- nce, to say nothing of the difficulties re raised in comparing data from the ture.

ere is dispute whether all non-arti- al disruptions on the crown surface e site of the Carabelli tubercle should garded as manifestations of the same opmental origin as the well-formed sory cusp or cuspule. Classically only ubercle or cusp has been considered e expression of the trait. However, e the turn of the century Batujeff 5), and later Mühlreiter and de Jonge n ('28), Hjelmann ('28), Dietz ('44), ro ('49), and Kraus ('51), have in- d pits and grooves occurring at the s phenotypic variations of the Cara- trait. Dahlberg ('51), on the other , contends that "the pit very likely is nnant of the cingulum and is prob- still confused with the cusp itself by workers on modern man." Because of onfusion in classification, compara- tive tables giving frequency distributions of the trait among various population groups are extremely difficult, if not impossible, to interpret (cf. table 33 in Dahlberg, '51, and table 21 in Pedersen, '49).

Among those investigators whose classifications include variable expressions of the Carabelli trait there is taxonomic disagreement. Shapiro ('49) suggests that the form of the groove rather than the shape or size of the tubercle be used as a basis for comparing racial incidence of Carabelli's trait. Dietz ('44), on the other hand, states: "A mere classification as to the type of cusp of Carabelli is valueless if its degree of development is not also included." He then proceeds to classify the tubercle itself as cuspoid, lobular, and ridged. De Jonge ('54) considers the pit as the weakest expression of the Carabelli trait.

There is general agreement on only one point with regard to the incidence of various expressions of the Carabelli trait in racial groups. All observers concur that in Mongoloids there is a very low frequency of Carabelli's tubercle. Because, however, of the great discrepancy in the method by which the various expressions of the Carabelli trait are dealt with, there is great difficulty in gaining more insight into the differential frequencies of occurrence of the trait in the various populations of the world.

In an earlier report ('51) the writer suggested a 4-fold classification of the Carabelli traits which will be followed in this paper. Briefly recapitulated, it is as follows:

1. PT — the pronounced tubercle whose tip is palpable.
2. ST — a slight tubercle, or bulge on the side of the tooth; the tip blends into the lingual crown surface.

3. GR — one or two grooves occurring at the site of the Carabelli tubercle.

4. P — one or two pits or fovea occurring at the site of the Carabelli trait.

As will be shown, these expressions may occur in various combinations on the same tooth. In this classification the various forms of the groove, such as Shapiro ('49) noted, are not distinguished.

In the present paper the distribution of the 4 Carabelli traits mentioned above will be indicated for several Southwestern ethnic groups, and a comparison of these frequencies will be made, where possible, with others recorded in the literature. It will be demonstrated that this classification will yield results consistent with the known history of these groups and will provide more meaningful comparative data.

NATURE OF THE DATA

All of the original data described in this paper are derived from prehistoric, historic, and modern populations of the State of Arizona. The prehistoric and historic skeletal material came from sites excavated by the Arizona State Museum. In all cases except the crania, dental impressions and plaster casts were made. The sample consisted of the following:

300 White school children in Tucson
274 Negro school children in Tucson
280 Papago Indian school children, examined at Sells
48 Apache Indian school children, examined at White River, and Cibecue on the Fort Apache Reservation
40 Yaqui Indian school children in Pascua
45 Prehistoric Arizona Indians, from various Pueblo III sites
19 Historic Indians from the San Jose site in Tucson
96 School children of Mexican ancestry in Tucson

A few words of explanation are necessary about the San Jose, the Prehistoric, the Apache and the "Mexican" samples. The San Jose material was excavated from a burial ground adjoining the ruins of a rancheria established by the Spaniards on the banks of the Santa Cruz River in what is now Tucson, Arizona. The skeletons pertain roughly to the period 1690–1800 A.D. The Prehistoric Indian sample belongs to the period 1050–1250 A.D. and represents the prehistoric Arizona Indian population of that period only in a very general way, since it derives from several archaeolo[gi]
sites in the Anasazi culture area. Im[p]
sions and casts of the Apache chil[d]
were made under difficult field condit[i]
so that it was inadvisable to examine
casts for the occurrence of pits. This
the only sample wherein pits were
recorded. The school children of Mex[i]
ancestry are United States citizens w[h]
parents or ancestors migrated from Mex[i]
Most commonly this ancestry consists
hybridization involving American In[d]
and European Whites.

RESULTS

The data will first be presented i[n]
general classification to be followed
more detailed breakdowns. In table 1
ethnic groups are lumped according
their affiliation with one of the three m[a]
racial stocks of mankind (Caucas[oid],
Negroid, and Mongoloid). In addition,
Tucson children of Mexican ancestry
designated as White-Indian hybrids. Th[e]
of the Carabelli traits are considered:
major manifestation (PT), an intermed[iate]
expression (ST, G, P, or any combina[tion]
thereof), and the complete absence of
expression (CA). This type of classifi[ca]
tion affords the easiest basis for comp[ar]
ison of the data with other recorded dis[tri]
butions in the literature. Table 1 indic[ates]
that Negroids and Caucasoids cannot
distinguished as populations by the Ca[ra]
belli traits. The Mongoloids, however,
significantly different from both Negro[ids]
and Caucasoids in having a higher
quency of intermediate expressions,
much lower incidence of pronounced tu[ber]
cles, and a slightly lower frequency of
sence of the traits. The White-Indian
brid group is distinguished from the ot[her]
three in having a much higher freque[ncy]
of expression, in one form or another.

TABLE 1

Frequency distribution of Carabelli expression[s] individual first permanent molars in Cauc[a]soids, Negroids, Mongoloids, and White-Indian Hybrids

Racial stock	No. of teeth	PT	STGP	
Caucasoids	600	0.162	0.393	0.[illegible]
Negroids	548	0.150	0.427	0.[illegible]
Mongoloids	882	0.015	0.611	0.[illegible]
White-Indian	96	0.146	0.656	0.[illegible]

arabelli expression. The types of ex- :on, however, are distributed differ- The frequency of PT is almost as as that of Negroes but the frequency ermediate expressions surpasses even of the Mongoloids.

ese data are in general agreement those reported in the literature. The 'T frequency of 1.5% for Southwest- ndians compares favorably with Ka- ; 3.4% for the Lapps ('12), Oshima's for Manchurians ('38), Pedersen's or East Greenland Eskimo ('49), and berg's 8% for the Pima Indians ('51). eater range for the PT frequency is :ent in the reports for Caucasoid os, but again the agreement with ıwestern Caucasoids is good. Batujeff 3) reports 10.3% for the Russians, erra ('05) 11.2% for the Swiss, Bolk 17.4% for the Dutch, Fabian ('28) % for the Germans, Kallay ('57) % for the Yugoslavs, Hillebrand (cited llay, '57) 13.6% for Europeans, Cor- cited in Della Serra, '51) 13.5% for guese, and Dietz ('44) 31.1% for icans, presumably all White. It must ointed out, however, that Dietz in- d in his "cuspoid" type also those cules which were minimally, moder- and maximally developed, so that percentage cannot be taken at face in this comparison.

is thus apparent that if the pro- ced tubercle is recognized as the only ession of the Carabelli trait one can ly distinguish between Mongoloid and asoid populations. Data on Negroid lations are too scarce to permit any :al conclusions, but it would appear that a classification based upon the three categories PT, STGP, and CA, cannot be used to separate Negroids from Caucasoids.

We turn now to a more detailed 5-point classification of the Carabelli manifestations and a breakdown of the sample into its constituent ethnic groups. In table 2 the frequencies of the three varieties of intermediate expressions are given separately, together with the PT and CA frequencies.

It becomes readily apparent that striking differences exist between certain of these ethnic groups. The frequency of pits is highest among Prehistoric and Papago Indians and ranges from 0 to 3.1% in the other groups. Whites have a relatively low percentage of grooves, while among Prehistoric, San Jose (Historic), and Apache Indians this expression is by far the most frequent one.

The frequency of slight tubercles groups Negroes, Papagoes, and Yaquis together. This observation is interesting in the light of certain speculations that have been made about Negroid mixture in both Papago and Yaqui populations. Seltzer ('36) has noted a number of Negroid features present in the Yaquis. These include: thick lips, dark skin color, jet-black hair, black eyes, heavy development of brow-ridges, preponderance of flaring nasal wings, high degree of frontal visibility of nostrils, broad nasal bridges, and retrogressive chin. Seltzer concludes: "It does seem evident that there is an element in the Yaqui population with a strong suggestion of certain Negroid features." Where and when this element entered the group is not known, but the possibility and signifi-

TABLE 2

'requency of occurrence of the various Carabelli traits in Southwestern populations, based on number of first permanent molars examined

Population	No. of teeth	PT	ST[1]	GR[1]	P[1]	CA
Vhites	600	0.162	0.290	0.092	0.012	0.444
Jegroes	548	0.150	0.150	0.246	0.031	0.423
'apago	560	0.020	0.150	0.334	0.080	0.416
pache	100	0.000	0.040	0.600	0.000	0.360
'aqui	81	0.012	0.160	0.482	0.012	0.334
'rehistoric Indian	98	0.000	0.051	0.633	0.102	0.214
an Jose	43	0.023	0.046	0.605	0.023	0.303

[1] When ST occurred with a pit or groove on the same tooth it was classified only as ST. Vhen GR occurred with one or two pits on the same tooth it was classified only as GR. ' may include one or two pits on the same tooth but is classified only once.

cance of the introduction of Negroid genes in American Indian populations has been clearly stated by Glass ('55):

"Nor ought one to conclude that because the Negro gene pool has relatively few American Indian genes, the converse is likewise true. That would by no means follow; for the American Indian populations being so much smaller and the tribes so much more isolated in mating than the American Negro population, it may well be that in certain Indian tribes the proportion of genes derived from Negroes is considerable .... the Indians were far more exposed to introgression of Negro genes than were Negroes to the introgression of Indian genes." pp. 382–383.

Both Seltzer ('36) and Gabel ('49) point out the affinity of Yaqui to Papago-Pima. Both Papago and Yaqui seem to retain certain non-Mongoloid features which might indicate retention of traits characteristic of the earliest American Indians who were, according to Hooton ('33) "a blend of Mediterranean, Negroid, and an Archaic White element, subsequently glossed over with Mongoloid traits."

Another interesting distribution comes to light in examining table 2. Absence of the Carabelli traits occurs more frequently among Whites, next among Negroes, less among living Indians, and least frequently among Prehistoric Indians. This is in direct contradiction to most of the statements made by other writers, many of whom, however, probably have considered all expressions except the tubercle as absence of the trait. It would be highly premature at this point to attempt to form any genetic hypotheses from these data.

From the material presented one might speculate, however, that the distribution of Carabelli traits among Prehistoric Arizona Indians was one of absence c pronounced tubercle, a high frequen intermediate expressions of the trait, low frequency of its complete abs Contact and subsequent intermixture Whites and White-Indian hybrids (cans) resulted in the introduction, at low incidence, of pronounced tuberc decrease in the frequency of interme forms, and an increase in the absen the trait. Modern Indians show change in this distribution. If anyt there is a continuation of the historic with respect to the intermediate form increase in the absence of the trait. data of the Apache offer no contradi to this generalization. The modern Ap reveal not a single instance of the nounced tubercle, but it has already noted (Kraus and White, '56) tha Apache of the Fort Apache Reserv show no evidence, serologically or s logically, of mixture with Whites.

Chi square tests applied to various p ethnic groups show some interestin sults (table 3). It is observed that the 5-point classification Whites Negroes can be differentiated, wherea previous 3-point classification sh them to be practically identical. Alth Negroid mixture at some time in the has been suggested for both Papago Yaqui Indians, apparently this postu mixture has become attenuated to point where there is no similarity bet these Indians and the Negroid grou the Carabelli distribution. On the hand the difference between Papago Yaqui is significant at slightly less the 5% level.

The difference between Papago Yaqui, on the one hand, and Apache, historic, and Historic Indians on the o

TABLE 3

Comparisons of frequency distributions of the five-point Carabelli classification in various paired ethnic groups by means of the χ^2 test

Paired ethnic groups	χ^2	D.F.	P
White-Negro	72	4	0.001
Papago-Yaqui	10.5	4	0.02–0.05
Prehistoric-Historic Indian	5.5	4	0.20–0.30
Apache-Historic Indian	4.8	4	0.30
Papago-Negro	76.4	4	0.001
Yaqui-Negro	26.2	4	0.001
Apache-Prehistoric Indian	13.9	4	0.01

very high order of significance. This to confirm the observations of Gabel ›eltzer based upon anthropometrics. icance tests indicated that the Apache [istoric Indian distributions could rep- : the same population. There is evidence that the San Jose site was ated in large part by an Apache band, his would account for the similarity en the two. On the other hand, the ıe, having little history of White ad- ıre, might be expected to show a ıl pre-contact distribution. That this usion is not borne out by the Cara- data is not surprising. The material senting our Prehistoric Indian sample obtained from archaeological sites in the same area now occupied by the ıe in east-central Arizona. However, l be recalled that the Apache are an ›ascan people who first entered the west about 400-600 years ago. The storic Indians of this sample are com- ıts of the Arizona Indian population e period 1050–1250 A.D. and were ntly the ancestors of the modern Zuni other Pueblo Indians. There would be no known biological relationship en the Apache and the Prehistoric na Indians other than the fact that are ultimately derived from Asia and have had no demonstrable mixture Whites.

ere has been comparatively little dis- on in the literature of the bilateral ssion of Carabelli's trait. Dietz found, 17 casts having both maxillary first rs, a bilateral expression of the "cusp rabelli" in all but 17 cases. He notes when "absent on one molar, it was minimally expressed on the other r." Bourdelle (cited by Della Serra, states that the tubercle is always eral. In the present series it was found the incidence of asymmetry varies in different populations from 6.7% to , without apparent pattern with re- to ethnic grouping. Among Whites Negroes, who have the highest ence of PT (16.2 and 15.0%, re- ively) the frequency of bilateral netry of this expression is 12.0 and % , respectively.

ateral absence of Carabelli's traits d presumably indicate the absence of the gene for expression of some form of the trait. Assuming a double allelic autosomal inheritance with dominance, the square root of the frequency of bilateral absence would give an approximation of the frequency of the allele "c." On this basis there would be little difference in the frequencies of "c" in these population groups. The highest frequency (see table 4) would be 0.062 (Whites) and the lowest 0.041 (Prehistoric Indians). Since the trait is inherited and populations are clearly distinguishable phenotypically and since there are similarities in frequency distributions between populations of the same racial stock, it is apparent that the mechanism of inheritance is either variable or more complex than has been suggested by this and other authors. For example, the low frequency of bilateral absence distinguishes Apache and Prehistoric Indians from the other groups studied. On the other hand, the Apache are significantly higher in the frequency of unilateral absence of the trait while the Prehistoric Indians are significantly lower in *this occurrence* than all other groups.[1]

Up to this point the frequency calculations have been based upon the occurrence on each individual maxillary first permanent molar. Slight tubercles, grooves, and pits have been lumped under the category "intermediate expressions." There is, perhaps, equal justification for lumping pronounced and slight tubercles, and distinguishing these expressions from surface invaginations such as pits and grooves. Considering PT and ST as manifestations of the maximum penetrance of the Carabelli genotype, and P and G as indications of moderate penetrance, let us count each individual once only, placing him in the category of maximum unilateral penetrance, that is, to be counted as CA an individual must have bilateral absence of the trait. If an individual has a left PT and a right G, he is classified as PT, etc. In other words we now revert to a threefold classification (table 4). This type of classification appears to be of maximum value since it best fits the available facts about these populations. The three major stocks of man are clearly separated. In

[1] Only the Yaqui are lower — by 1.7% — in frequency of unilateral absence.

TABLE 4

Frequency distribution according to maximum bilateral expression of the Carabelli trait

Ethnic group	PT and ST	P and G	CA
Whites	0.500	0.113	0.387
Negroes	0.339	0.296	0.365
Papago	0.225	0.422	0.353
Yaqui	0.214	0.477	0.309
Apache	0.083	0.709	0.208
Historic Indians	0.083	0.709	0.208
Prehistoric Indians	0.057	0.773	0.170

addition, a distinction emerges between the Prehistoric Indians on the one hand, the Historic and Modern Indians on the other. Moreover, the historically attested affinity between the San Jose (Historic) and Apache populations is indicated. The Apache, who are linguistically, serologically, and historically distinct from both Yaqui and Papago, can be easily distinguished by means of the three-point classification of the Carabelli trait. The frequency distributions of the three Carabelli expressions among the Papago and Yaqui are so similar that they afford support for the suggested biologic affinities of the two peoples advanced by Seltzer and Gabel. At the same time the Papago-Yaqui frequency distribution of the Carabelli trait is not unlike that of the Negro sample, which calls to mind the anthropological observations of Seltzer and Gabel hinting at Negroid admixture with these two Indian groups.

The above data are not adequate to attempt a genetic interpretation but certain tentative general conclusions might be advanced. If we are correct in ascribing such morphological features as pits, grooves, slight tubercles and pronounced tubercles to a common locus (or loci), then it would appear that the allele (or alleles) responsible for a Carabelli expression is more common among unmixed Mongoloids than among Whites or Negroes. The Mongoloid genotype, however, does not achieve maximum expressivity, for reasons which are not yet known. Instead, it results in a high frequency (75%) of pits and grooves and a very low frequency of slight tubercles (5%). The pronounced tubercle was not found in the Prehistoric Arizona Indians or in Pedersen's ('49) East Greenland Eskimos, both of whom represent unmixed Mongoloid populations. When the posing genotype is present it may ex itself unilaterally only or bilaterally. I latter case the expressions may be metrical or asymmetrical. This sug the presence of modifying genes.

When there is White admixture in goloid populations the effect is three There is a slight increase in the frequ of maximum expressions (PT and ST slight decrease in the frequency of i mediate expressions (G and P), a slight increase in bilateral absence of expression. Continued admixture (am unknown) results in an intensificatio this trend (Papago and Yaqui). In the of Whites there is a relatively high quency of bilateral absence, a high quency of maximum expression, and a low frequency of intermediate expres An hypothesis of two allelic autos genes without dominance (Kraus, '51) been advanced to account for inherit of the Carabelli trait in Caucasoids, only if ST, G, and P are considered var expressions of a heterozygote genotyp perusal of phenotypic frequencies in ples of the three major stocks of man gests that this hypothesis is not adeq to explain all the observations.

Two lines of approach are clearly c for. Observations of the Carabelli should be made on well-defined bree populations representing each of the m human stocks, with all variants of the pression carefully recorded. In addi pedigrees should be collected in each o major stocks so that a more defin genetic interpretation can be produ We could then look forward to a sou understanding of the effects of hybrid tion on the Carabelli phenotype distr tion. There is every reason to expect this trait will become one of the m valuable additions to the armamentar of the student of human micro-evoluti

CONCLUSIONS

The dentitions of samples of sev ethnic groups, representing prehisto historic, and modern peoples of Arizo were studied and the expressions of Carabelli trait on the mesiolingual cr aspect of the maxillary first perman molar were noted. The expressions w

ıed in several ways in an attempt to ve a classification which yielded in- ıtion consistent with what is known gically and anthropologically about populations. In addition, compara- lata recorded by earlier writers were dered.

was found that there was generally agreement with the data collected ghout the world on the basis of fre- cy distributions of the variable Cara- expressions for Caucasoids and Mon- ds. There were insufficient data for Negroid populations.

phenotypic classification which lumps ounced and slight tubercles as forms aximum penetrance of the trait, pits grooves as expressions of intermediate rance, and bilateral absence as indi- g absence of the disposing genotype, found highly adequate for discriminat- he Southwestern ethnic groups ac- ng to available populational informa- Unmixed Mongoloid populations a low frequency of absence of the as well as of maximum penetrance, very high frequency of intermediate rance. Whites, on the other hand, a high frequency of maximum pene- e, a very low frequency of intermedi- penetrance, and a relatively high ency of absence. The introduction of e genes in Mongoloid populations ap- to change the phenotypic distribution rds the White spectrum.

ntrary to what has been implied in iterature, Mongoloid populations may a higher frequency of the Carabelli (or genes) than do Whites, although fying genes appear to change the e of the expression. It is suggested more definitive populational and pedi- studies will eventually make the Cara- trait an important tool for research in o-evolution.

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ɔngitudinal Study of Growth in Face Depth ing Childhood[1]

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is report pertains to an anteroposte- limension of the facial skeleton in ı *sapiens.* Its data are drawn from *a lateralis* roentgenograms for 125 children examined at annual inter- ɪetween the postnatal ages of 5 years 11 years. Previous studies of the .n osseous face, similar in method :overing the same segment of ontog- have dealt with growth in a trans- dimension (Newman and Meredith, and a vertical dimension (Meredith,

OBJECTIVES

e goals in making the present study

To define a measurement of skeletal depth for which highly reliable re- could be derived radiographically.
To accumulate, using the procedure ɘd, seriate records of skeletal face extending over the childhood period age 5 years to age 11 years.
To investigate skeletal face depth rt by analyzing measures of absolute or variability and trend, and in part ıalyzing increment data for velocity ences and correlation with compa- data for other facial variables.

e anteroposterior facial dimension ed for study may be identified :ively as the rectilinear distance from ıost forward point on the anterior spine to a point near basion (the :ior landmark will be described pre- in a later paragraph). The plan of tions may be characterized as one ɔped to secure findings with respect 6-year period of childhood for (1) of mean skeletal face depth on age, ⁄ariability of skeletal face depth at ed ages, (3) differences among in- ıals in trend, absolute increment, and ntage gain, and (4) associations be- tween changes during corresponding age intervals in depth, breadth, and height dimensions of the face.

SUBJECTS

The subjects were 60 boys and 65 girls residing in or near Iowa City, Iowa. All were voluntary participants in the Facial Growth Study, a long-term research program at the State University of Iowa begun in 1946 under the joint sponsorship of the Department of Orthodontics and the Iowa Child Welfare Research Station. Enrollment in the study was based on likelihood of continuing residence in the community and willingness to participate; it was not related to odontic condition or need for orthodontic treatment.

The 125 subjects constitute a group of American-born white children predominantly of northwest European ancestry and above average socioeconomic status. More than 90% of the subjects had three or more grandparents of northwest European descent; the others had two or more grandparents of central or southeast European background. Information on vocation showed that approximately 50% of the fathers held professional or major managerial positions; 40% owned small businesses, followed skilled trades, or engaged in commercial occupations; and 10% were semiskilled employees.

Every subject was examined annually from age 5 years to age 11 years. The examinations were made on or near each child's birth anniversary.

MATERIALS AND METHODS

Data for depth of the osseous face were derived from roentgenograms obtained

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with the child's head positioned in a cephalostat (Krogman and Sassouni, '57). The x-ray source was to the right of the child at a distance 150 cm from the median plane of the cephalostat, the cassette was near the left side of the child's head, and the central ray passed through the child's external acoustic meatuses perpendicular to the sagittal plane and the plane of the film.

Two landmarks were sought on each roentgenogram. These were defined as (1) the most forward point on the radiographic image of the anterior nasal spine, and (2) the most forward point on the radiographic image of the occipital condyles. Under conditions of symmetrical development of the condyles, and correct subject orientation for a *norma lateralis* roentgenogram, the posterior landmark may be described as the site of junction of the anterior margin of the *right* occipital condyle with the precondylar portion of the occipital bone. Adequate representation of the tip of the anterior nasal spine was provided for by use of an aluminum wedge at the time of film exposure.

In order to minimize age-to-age variation in landmark determination, a landmark was registered at a single sitting on the entire series of roentgenograms for a subject. This was done with the aid of an illuminated worktable and a magnifying glass, each roentgenogram being pricked with a fine-point probe.

The rectilinear distance between the two marked termini was measured by means of a steel tape read to the nearest 0.01 cm. Roentgenograms were taken for measurement in random order, and each was measured by two anthropometrists working independently. When the two independent records agreed within 0.02 cm, they were averaged. In instances of greater discrepancy, two additional measurements were taken and either the mean of the 4 determined or, where there was an obvious misreading of the scale, the mean of the homogeneous three.

Each obtained value was corrected for radiographic enlargement. An earlier publication (Newman and Meredith, '56) describes in detail the procedure by which the appropriate adjustments were made. The adjusted values represent skeletal face depth defined as the minimum dis[tance] from the tip of the anterior nasal [spine] (TANS) to the anteriormost point o[f the] occipital condyles (APOC). On occa[sion] this dimension will be referred to as T[ANS-]APOC diameter.

Had it been possible to measur[e the] rectilinear distance from the tip o[f the] anterior nasal spine to basion, prefe[rence] would have been given to this dimen[sion.] Since basion cannot be identified o[n a] *norma lateralis* roentgenogram (B[j...] '47), the measure of face depth obtai[ned is] a close substitute.

Meticulous care was taken to o[btain] valid data for the diameter stu[died.] Chance errors were minimized by rig[id] controls in subject positioning, land[mark] location, and measurement; anatomi[c rel]evance was enhanced by precisely cor[rect]ing for the systematic errors that ra[diog]raphy imposed.

Trend of means for sex groups

Columns 2 and 5 of table 1 displa[y] means for skeletal face depth obtaine[d for] each age-sex subgroup. In figure 1 t[hese] values are plotted and the trend of m[eans] for each sex portrayed. Considering [the] tabular and graphic presentations joi[ntly] and drawing from prior research for [com]parative purposes, the following find[ings] may be listed:

1. Over the childhood period betw[een] age 5 years and age 11 years, the comp[...]

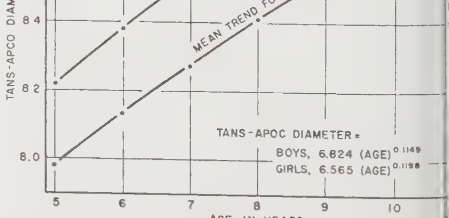

Fig. 1 Curves drawn to means for ske[letal] face depth on North American white chil[dren,] 60 boys and 65 girls, studied longitudinally.

mass *trend* for absolute size of the dimension under study is an ascend- ırve slightly concave to the chrono- base line. In other words, the group itude trend for TANS-APOC diameter ı upward slope of slowly diminishing ıess.[2] It also has been found that the ologically comparable biomass trends keletal bigonial diameter (Newman Meredith, '56) and skeletal nose t (Meredith, '58) are negatively ac- ted increasing functions of age.[3]

For each sex, the series of means on represented satisfactorily by a para- equation. The calculated formulas, d by the method of least squares, are $\times$ Age in years$^{0.1149}$ (boys) and $\times$ Age in years$^{0.1198}$ (girls). Accept- 'goodness of fit" is indicated by the g that corresponding means, obtained stimated from formula, in no instance by more than 0.02 cm. In the previ- cited studies of bigonial face breadth nose height, parabolic equations ating obtained means met a similar ion of adequacy in estimation.

At each age, the mean for TANS- C diameter is larger on boys than on A significance test at age 5 years des grounds for rejecting, at a high of confidence, the hypothesis of m sampling from a common popula- $t = 4.32$, *df* 123). The amount of the ifference does not change with age, it is 0.25 cm at 6 years, 0.25 cm at ırs, and 0.24 cm at 10 years. Ex- pressed in relative terms, the central tendency statistics of this study show that during the childhood period between 5 to 11 years of age the face depth of the average girl is smaller than that of the average boy by approximately 3%.

4. The table 1 means at age 11 years are higher than those at age 5 years by practically the same amounts for boys and girls. Combining the sexes, the mean at age 11 (8.88 cm.) exceeds that at age 5 (8.10 cm) by 0.78 cm. The relative increment with respect to mean magnitude at the beginning of the 6-year period ($0.78 \times 100/8.10$) is 9.6%. Comparable percentage increases for skeletal bigonial diameter (Newman and Meredith, '56) and skeletal nose height (Meredith, '58) are 13.7 and 19.6, respectively. Colligating: during childhood relative growth rates are highest for the vertical dimension, intermediate for the transverse dimension, and lowest for the anteroposterior dimension.

5. Over successive biennial portions of the age span covered, absolute increases in mean face depth (both sexes together) are 0.30 cm, 0.25 cm, and 0.23 cm. The reader is reminded that in longitudinal research the difference between means at two ages is identical with the mean of the

[2] For discussions of the terms "biomass" and "trend," see Medawar ('50) and Sholl ('54), respectively.

[3] A function that increases at a declining rate is described as "negatively accelerated" since its first derivative has a negative exponent.

TABLE 1

Central tendency and variability statistics for a measure of skeletal face depth (TANS-APOC diameter in centimeters)

Age in years	Boys: N = 60			Girls: N = 65		
	Arithmetic mean	Standard deviation	Coefficient of variation	Arithmetic mean	Standard deviation	Coefficient of variation
5[1]	8.22	0.30	3.7	7.98	0.31	4.0
6	8.38	0.32	3.8	8.13	0.32	4.0
7	8.53	0.32	3.8	8.27	0.33	4.0
8	8.66	0.34	3.9	8.41	0.34	4.1
9	8.78	0.35	3.9	8.53	0.36	4.2
10	8.89	0.36	4.0	8.65	0.37	4.3
11	9.00	0.37	4.1	8.77	0.39	4.4

[1] The reader may wish to interpret the statistics for a particular age-sex subgroup as arameter estimates. Standard errors of the A.M. are 0.04 cm (ages 5 through 8 years, boys; through 9 years, girls) and 0.05 cm (ages 9 through 11 years, boys; 10 and 11 years, girls). he standard error of the S.D. is 0.03 cm in each instance. Standard errors of the C.V. re 0.3% (ages 5 through 7 years, boys) and 0.4% (8 through 11 years, boys; 5 through 1 years, girls).

individual changes between the two ages, i.e., the mean absolute gain in TANS-APOC diameter for the age interval 5 to 7 years is 0.30 cm, and so forth. Consecutive biennial percentage gains for the entire sample, again applying the Minot ('08) formula,[4] are 3.7, 3.0, and 2.7, respectively.

In investigations utilizing direct measurements of the face, the anteroposterior dimension that has received most study is distance from the transmeatal axis to prosthion (Hellman, '27; Smyth and Young, '32; Goldstein, '36; Allen, '48; Henriques, '53). Another dimension employed to some extent, and having its anterior terminus closer to TANS, is porion-subnasale diameter. This diameter was studied by Henriques ('53), using data obtained from measuring the face directly, and by Allen ('48), using estimates of direct face measurement derived from roentgenograms. The subjects for both investigations were elementary school children. Allen's sample was drawn in the British Isles and supplied means for each sex at ages 6 and 7 years; Henriques' sample was drawn in North America (Philadelphia) and supplied means for each sex at annual age from 7 through 11 years. All of these values are smaller than comparable subgroup means for TANS-APOC diameter; on the average, the systematic differences approximate 0.55 cm (Allen study) and 0.20 cm (Henriques study).

Variability at selected ages

Statistics depicting the variability of skeletal face depth are presented in tables 1 and 2. Table 1 epitomizes the dispersion for each age-sex subgroup in terms standard deviation and the coeffici variation. In table 2 the spread of butions for each sex at 4 selected a displayed in terms of the extreme and several spaced percentiles. Fin descriptive and comparative, are:

1. During the childhood period age 5 years to age 11 years there gradual increase in the variability of T APOC diameter. The standard devi for boys rise from 0.30 cm at 5 through 0.34 cm at 8 years, to 0.37 11 years; those for girls are of s magnitude and rise in like manner 1). An increase with age in absolute ter also was found by Newman Meredith ('56) in their study of sk bigonial diameter.

2. TANS-APOC diameter has a index of relative variability than sk nose height. The coefficient of var for skeletal face depth on boys age 5 is 3.7% of mean face depth at thi (table 1). A corresponding statist 5.7% for skeletal nose height was se by Meredith ('58). The coefficient tained on girls age 5 years are 4.0% 5.2% for face depth and nose he respectively.

3. Age-specific distributions of depth on boys, although centered syste ically to the right of those on girls tensively overlap the girls' distribu (table 2). At age 7 years, for exam TANS-APOC diameter is (a) less 8.7 cm in 70% of the boys compared

[4] Absolute change in size between two × 100/Absolute size at the initial age.

TABLE 2

Variability statistics for skeletal face depth measured as TANS-APOC diameter in centimeter

Age in years	Minimum	Percentiles 10	30	70	90	Maximum
		Boys: N = 60				
5	7.5	7.8	8.0	8.4	8.6	9.1
7	7.8	8.1	8.3	8.7	8.9	9.4
9	8.0	8.3	8.6	9.0	9.2	9.7
11	8.1	8.5	8.8	9.2	9.4	9.9
		Girls: N = 65				
5	7.3	7.5	7.8	8.1	8.4	8.8
7	7.6	7.8	8.1	8.4	8.7	9.1
9	7.8	8.0	8.3	8.7	9.0	9.4
11	8.0	8.2	8.5	8.9	9.2	9.7

of the girls, and (b) more than ı in 90% of the boys compared with of the girls.

There is extensive overlapping of x-specific distributions for skeletal lepth at successive ages. Measure- of TANS-APOC diameter below ı are secured on 30% of the girls at years and 10% of those at age 7 Similarly, face depth measurements 9.2 cm are secured on 90% of the ıt age 9 years and 70% of those at l years.

The distribution of skeletal face for boys of a given age is similar to or girls two years older. Inspection le 2 shows that the 10th percentile is me on boys age 5 years, and girls age s; the 30th and 70th percentiles are me on boys age 7 years, and girls age s; the 90th percentile is the same for ıge 9 years, and girls age 11 years; o forth.

le 2 may be regarded as providing s of reference for TANS-APOC diam- So regarded, it augments the tabu- d graphic norms on North American children presently available to rs in applied anthropology (Mere- 59). From this perspective, the per- es of table 2 partition each distribu- ıto 5 sections. A child whose skeletal epth is below the 10th percentile for e and sex falls in the lowest of the ions, and may be designated as hav- shallow face. Proceeding along the uum, children falling between per- es 10 and 30, 30 and 70, 70 and 90, bove 90 may be designated, in this as having faces that are moderately w, average, moderately deep, and

Trends for the individual

procedure employed in studying in- ıal magnitude trends for skeletal face was as follows:

The seriate data for each subject plotted on a separate Cartesian grid. cutive annual ages were the abscissa and corresponding measurements of -APOC diameter the ordinate values. A curve was drawn connecting the ted points representing a child. As vious studies of individual growth in al bigonial diameter and skeletal nose height (Newman and Meredith, '56; Meredith, '58), each time series for skeletal face depth consisted largely of a trend, i.e., curve irregularities were few and minor.

3. The 125 graphs were compared and sorted with respect to trend similarities and differences. This step generated the decision to discuss findings on varieties of trend with the aid of illustrations for three subgroups (fig. 2) and 4 individuals (fig. 3).

The trend of subgroup A in figure 2 was derived by calculating age means for the annual measurement of TANS-APOC diameter on 27 children, 12 boys and 15 girls. Over the sexennium from age 5 years to age 11 years, these children each exhibited

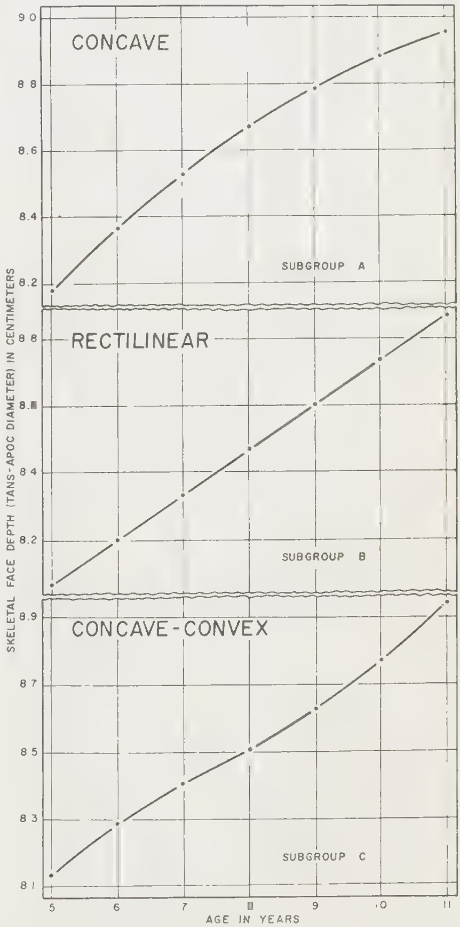

Fig. 2 Trends drawn to means obtained after subgrouping individual curves for skeletal face depth.

an ascending trend that satisfied explicit criteria regarding concavity to the chronologic base line. For every child included in the "concave" subgroup it was required: (1) increase in face depth between ages 5 and 7 years exceed that during the next biennium by 0.05 cm or more, and (2) increase in face depth between ages 7 and 9 years exceed that during the succeeding biennium by 0.05 cm or more.

Annual measurements of TANS-APOC diameter on 23 children, 11 boys and 12 girls, were used in obtaining the mean trend for the "rectilinear" subgroup. The separate graphs of these children depicted oblique lines each rising at an approximately constant velocity. For inclusion in this subgroup, it was specified th difference among a child's increme the bienniums 5 to 7 years, 7 to 9 and 9 to 11 years surpass 0.03 cm.

The "concave-convex" trend sho figure 1 was secured by averagin skeletal face depth measurements nual ages for 11 children, three boy 8 girls. These children comprise a geneous subgroup in that each of gained 0.05 cm or more between 11 years of age than during the prec biennium. That is, subgroup C inc every subject who, *in late childhooc* an ascending curve unequivocally c to the chronologic base line. For th period from 5 to 11 years, the indiv

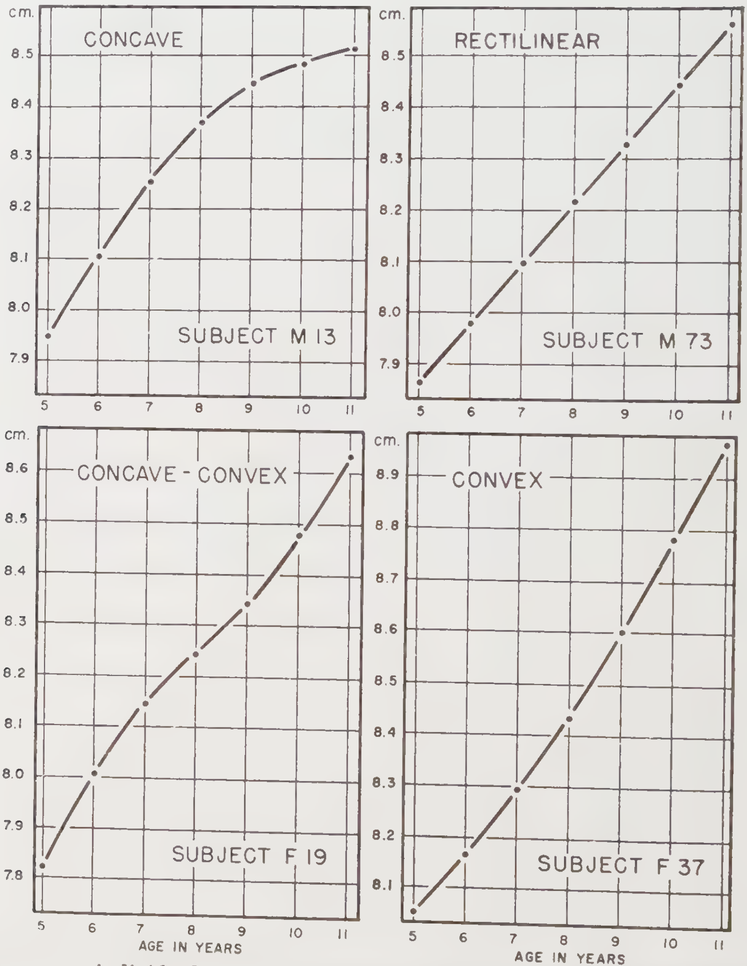

Fig. 3 Curves on individual children depicting varieties of trend for skeletal face depth.

; are "concave-convex" in 7 instances, rectilinear-convex" or entirely "con- n 4 instances.

ure 3 was compiled by selecting one from subgroup A, one from subgroup l two from subgroup C. Selection was to portray pronounced examples of ies of individual magnitude trend ce depth.

ty-four of the 125 trends for individ- ıre not represented in figure 2 and l of these constitute intergrades be- the concave and rectilinear trends yed in figure 3.

findings of this study from analysis ividual magnitude curves for skeletal depth may be complemented with from earlier analyses for skeletal ial diameter (Newman and Mere- 56) and skeletal nose height (Mere- '58). Descriptive and comparative gs, specific for the child population egment of ontogeny investigated, are:

All of the individual curves for -APOC diameter ascend in some y oblique manner. Likewise, individ- urves for osseous measurements of readth and nose height lie in paths ing overall increase in size with age.

Approximately 90% of the trends eletal face depth rise rectilinearly or vely to the chronologic base line. arly, between 85% and 95% of the s for skeletal bigonial diameter and al nose height climb along routes ıg from straight-line paths to curvi- paths concave downward.

Approximately 70% of the curves eletal face depth manifest a general ment of ascent with declining veloc- Most of these curves are "concave" ghout. Some are concave during the ne-third to one-half of the sexennium ectilinear thereafter. The "concave" dual trend also is the commonest found for skeletal bigonial diameter skeletal nose height: relative fre- cies fall between 65% and 75%.

The relative frequencies for rising inear trends, again assembling find- on the osseous face from investiga- of an anteroposterior dimension, a verse dimension and a vertical dimen- fall between 15% and 25%. For TANS-APOC diameter, the figure approximates 20%.

5. Individual trends convex to the chronologic base line between ages 9 and 11 years have relative frequencies below 5% for skeletal bigonial diameter, near 10% for skeletal face depth, and near 15% for skeletal nose height. "Convexity" over the period from 9 to 11 years for bigonial diameter, and over the period from 5 to 11 years for any of the three dimensions, (see figure 3, subject F37), are rare phenomena.

Velocity differences

This section presents findings on inter- and intra-individual differences for rate of growth in TANS-APOC diameter. It (1) describes the variability of increment distributions, (2) displays increment variations by superimposing magnitude trends, and (3) investigates the association between increments for two age trienniums.

Absolute increments (changes in centimeter terms) were derived on each subject for three consecutive biennial intervals and the full 6-year interval. To illustrate: from the time series for skeletal face depth on child X, differences were obtained between the measurements at ages 5 and 7 years, 7 and 9 years, 9 and 11 years, and 5 and 11 years. In addition to centimeter increases, percentage increases (using the Minot formula) were computed.

When these data were tabulated in frequency distributions according to sex, age interval, and type of increment, it was found that comparable distributions for boys and girls did not differ significantly. Consequently, the distributions were collapsed for sex. Statistical reductions of the 8 distributions remaining are assembled in table 3. Selected findings are:

1. Absolute gains in TANS-APOC diameter during the period from age 5 years to age 7 years are between 0.14 cm and 0.22 cm for 10% of the children, between 0.27 cm and 0.33 cm for 40%, and between 0.38 and 0.53 cm for 10%. Relative gains during the same period extend from a minimum of 1.8% to a maximum of 6.2%, with four-fifths of them clustered between 2.7% and 4.6%.

2. Velocity distributions for the biennium from 9 to 11 years of age are sys-

tematically lower than those for the biennium from 5 to 7 years of age. Gains exceeding 0.27 cm are made by 70% of the children between ages 5 and 7 years, compared with 30% between ages 9 and 11 years. No child's increment is below 1.8% during the earlier biennium, although during the later biennium 10% of children increase less than this.

3. Over the sexennium from age 5 years to age 11 years, some children augment their skeletal face depth more than twice as much as other children. Absolute gains are less than 0.5 cm for 5% of the sample, and 1.1 cm or more for 4%. For similar portions of the sample, relative gains are less than 6.0% and more than 13.0%, respectively.

Figure 4 portrays two pair of individual magnitude curves selected to illustrate markedly different amounts of growth in TANS–APOC diameter. Contrast A utilizes the time series on subjects F15 and F81. Subject F81 is the child showing the least absolute change in face depth between ages 5 and 11 years (see table 3, row 4). The other subject is a child matching F81 with respect to (a) sex and (b) face depth in early childhood, but differing widely from F81 in absolute increment. F81's increase of 0.28 cm between 5 and 11 years of age is (1) smaller than F15's increase of 0.42 cm for the biennium 5 to 7 years and (2) only one-fourth F15's increase of 1.11 cm for the entire sexennium.

The time series on subjects M67 M78 are used in figure 4, contrast B. ject M78 is the child registering the imum relative increase in TANS- diameter between 5 and 11 years (see table 3, row 8). The other subj a child matching M78 with respect t sex and (b) face depth in middle hood, yet differing greatly from M relative growth rate. The sexennial ment of 14.2% for the fast growin is two and one-half times that for the growing boy (5.7%). Compared i other manner, the face depth relati these two boys is transposed from th M78 being the smaller at 5 year 0.31 cm, or 3.9%, to that of M67 bein smaller at 11 years by 0.35 cm, or 4.

Meredith and Meredith ('58) in gated associations in childhood bet measures of body size and measur growth rate. For skeletal face depth, found that neither the absolute no relative increments of individual chi during the period 5 to 11 years of age be forecast satisfactorily from info tion on size at age 5 years. The r rep for covariation of skeletal face depth years and centimeter gain over the en sexennium is 0.13. With percentage replacing absolute gain, $r = 0.02$. coefficients disallow rejection of the thesis that the population r is zero consequently, are valueless for the pu

TABLE 3

Variability of increase in TANS-APOC diameter for three biennial periods and a sexennial period

Age interval in years	Minimum	Percentiles				Maximu
		10	30	70	90	
		Centimeter increase				
5–7[1]	0.14	0.22	0.27	0.33	0.38	0.53
7–9	0.09	0.16	0.22	0.29	0.32	0.40
9–11	0.01	0.15	0.20	0.27	0.32	0.44
5–11	0.28	0.58	0.71	0.88	0.99	1.21
		Percentage increase[2]				
5–7	1.8	2.7	3.3	4.1	4.6	6.2
7–9	1.1	2.0	2.7	3.4	3.9	4.6
9–11	0.1	1.8	2.3	3.1	3.7	4.8
5–11	3.5	7.2	8.9	10.7	12.2	14.2

[1] Each distribution consisted of increment values for 125 North American white childre of both sexes.

[2] Computed as: Centimeter gain in skeletal face depth during the period indicated × 100 Magnitude of skeletal face depth at the beginning of the period.

izing a child's attained size to pre-
s subsequent growth rate.
he present study, another question
rning the predictability of velocity
nces was investigated: With what
of precision can children's rates of
in TANS-APOC diameter between
and 11 years be forecast from their
rates during the preceding trien-

statistic obtained from correlating
eter increases for the periods 5 to
s and 8 to 11 years (N = 125) is
50. Concomitant variation of per-
e gains for the same triennial pe-
lso is represented by $r = 0.50$. Two-
le rectilinear regression equations
ped with coefficients of this magni-
ave a low index of forecasting effi-
, E = 13.4% (Guilford, '50).
regard to predicting *absolute incre-*
in skeletal face depth between 8 and
ars of age, the standard error of
te is (a) 0.098 cm from unvarying
the mean increase for the period 8
years and (b) 0.085 cm from enter-
e child's increase between 5 and 8
in the best-fit regression equation.
quation is: centimeter gain, 8 to 11
= 0.56 (centimeter gain, 5 to 8
) + 0.14. It follows that this equation affords an improvement of 13.4% on the "best guess" standard error of 0.098 cm. The same small improvement in predicting *relative increments* accrues with reduction of the standard error of estimate from 1.04%, when the mean relative increase is used, to 0.90%, when use is made of the best-fit regression equation, i.e., percentage gain, 8 to 11 years = 0.48 (percentage gain, 5 to 8 years) + 2.52.

Growth rate associations for three facial dimensions

In this section consideration is given to relationships among absolute and relative increments for a trio of anteroposterior, vertical and transverse dimensions of the upper face. The three traits are TANS-APOC diameter, nasion-TANS diameter, and bizygomatic diameter. Previous publications give detailed description of the procedures by which the data for nasion-TANS diameter (Meredith, '58) and bizygomatic diameter (Meredith, '54) were procured. Reiteration is unnecessary beyond notation that the methods used in obtaining the basic measurements were adequate to assure highly reliable increment data representing the segment of childhood between ages 5 years and 11 years. For

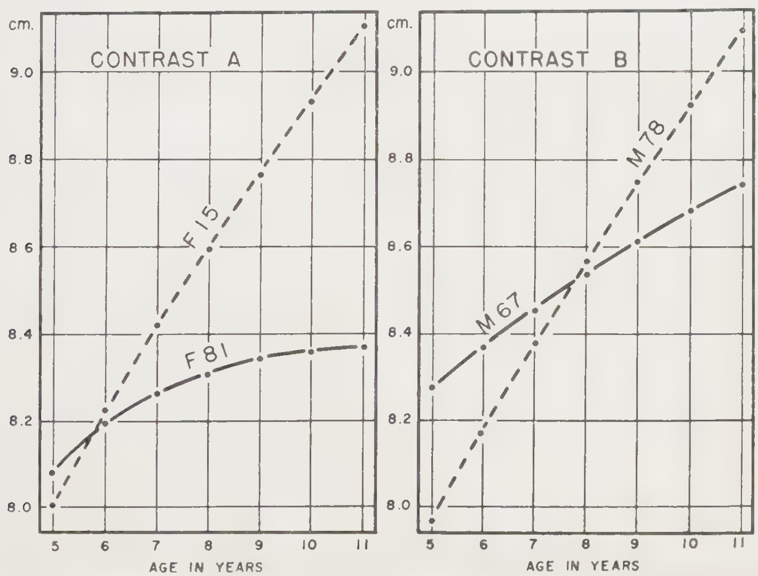

Fig. 4 Trends illustrating individual variation in amount of growth in skeletal face depth
tween age 5 years and age 11 years.

all of the associations that will be reported, N = 125.

Dealing first with covariation of the face depth and nose height variables, the obtained r's are 0.13 from correlating centimeter gains and 0.12 from correlating percentage gains. Neither value allows rejection of the hypothesis that the growth rate populations are independent. With 123 *df*, it is required that a r statistic exceed 0.17 for rejection of this hypothesis at the 5% level of confidence (Lindquist, '40).

Concomitant variation of the face depth and bizygomatic face breadth variables is low positive. The specific r's secured are 0.36 for covariation of the absolute increments and 0.33 for covariation of the relative increments. Both coefficients exceed the value necessary for rejection of the null hypothesis at the 1% confidence level (r greater than 0.23, 123 *df*).

The correlation statistics obtained from the nose height and bizygomatic face breadth variables are $r = 0.22$ (absolute increases) and $r = 0.21$ (percentage increases). On the assumption of random sampling, it is tenable at the 5% confidence level to infer that these coefficients have not arisen from zero related populations.

It follows that there is little association among growth rates for the three dimensions. In no instance can change in one of the dimensions during the sexennium of childhood between ages 5 years and 11 years be predicted satisfactorily from change in one or both of the other dimensions. Estimation of centimeter gain for bizygomatic face breadth from centimeter gain for face depth, employing $r = 0.38$ in deriving the best-fit rectilinear regression equation, would have a long-run efficiency (E) below 7%. Estimation of centimeter gain in bizygomatic face breadth from centimeter gains in face depth and nose height would be almost as poor (the multiple correlation coefficient representing this relationship, R = 0.41, is associated with E = 8.8%).

In an analysis of velocity data for bizygomatic face breadth and bigonial face breadth covering the period from age 5 years to age 11 years, Newman and Meredith ('56) found covariation "is positive and approximates the order $r =$ This relationship between increas transverse diameters of the uppe lower face is as high as any combinat increases for the three traits measu different planes of the upper face.

Incidental study was made of the a ation between absolute and relative ments for a given dimension. The tained are 0.98 from the face depth ments, 0.97 from the bizygomatic br increments, and 0.94 from the incre for nose height.

SUMMARY

A measurement of skeletal face is investigated with respect to size change during the second sexenniu human ontogeny. Absolute magni data are analyzed longitudinally for and cross-sectionally for variability solute and relative increments are us study velocity differences and associa with changes in other measuremen the face.

The subjects are 125 American white children predominantly of nort European ancestry and above av socioeconomic status. On each su highly valid measures of face dept derived from *norma lateralis* roent grams obtained at annual interval tween age 5 years and age 11 years. time series for face depth are supplem with increment data on the same chi for bizygomatic face breadth and sk nose height.

It is found: (1) the trend of mean face depth in childhood is a nega accelerated increasing function of age at each age studied average face dep larger in boys than girls by approxim 3%, (3) both absolute and rel variability of face depth increases wit (4) approximately 90% of indiv magnitude trends for face depth rise cavely to the time base line or as obliquely to the time base line, (5 creases in face depth during childhoo more than 100% larger in some ind uals than in others, (6) the associatio tween rate of growth in face depth 5 to 8 years of age and rate of growth 8 to 11 years of age approximates 0.50, (7) relationships among absolu

ents for face depth, face breadth and
height lie between zero and $r = 0.40$,
(8) concomitant variation among
ve growth rates is no higher than
g absolute growth rates.

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e Skin of Primates

THE SKIN OF THE POTTO (PERODICTICUS POTTO)[1]

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ie skin of man has many unique fea- that are difficult to relate to those e skin of other mammals. (1) It has ick, distinct and richly vascularized llary body; (2) the underside of its ermis is thrown into a complex sys- of ridges and valleys, craters and nds; (3) numerous eccrine sweat ds are distributed over the entire body ace; whereas (4) apocrine sweat ds are few and restricted to character- sites; (5) the cavum axillae is a rich of large apocrine glands intermingled eccrine sweat glands, the two types lands constituting the axillary organ; the scalp has numerous sweat glands, the hair follicles there have a longer of growth than those elsewhere; also, calp of the ageing male has a tendency ecome bald. In contrast, the skin of mammals that we know anything t, excluding primates, (a) has a thin poorly vascularized papillary body; the underside of the epidermis is lly flat; (c) eccrine sweat glands, if ent, are restricted to the volar side of ands and feet; (d) when sweat glands present over the body surface they are e apocrine type; (e) an axillary organ not been found; (f) the skin of the shows none of the peculiarities of the of man. One wonders if the unique- of human skin is real or apparent, to what extent man shares with other ates the pecularities of his skin.

though all mammals have a basically lar skin, each of the major orders has acteristic differences, and differences even exist within the same order. the recognition of the pecularities in skin of a single group, the more gen- zed patterns, which are probably re- to an ancestral type, should become evident. Thus, systematic comparative studies of the skin in the members of a family or order may turn up different modifications of cutaneous structures and provide information on phylogenetic relationships. This report is the first in a series which will describe the skin of primates. In identifying the many adaptations in this order, we hope to point up the basic underlying patterns which will be valuable points of reference to students of evolution, comparative physiology, systematics, experimental biology, and dermatology.

The German literature contains a surprisingly large number of studies on the skin of primates. These studies are concerned mostly with the color of skin and hair, with the types and the density of population of hairs, and with dermatoglyphics. Some studies have dealt with the sweat glands, and particularly with those of the axilla. Most of this literature, however, is relatively ancient and fragmentary. Moreover, the majority of these studies were carried out on material of dubious quality for histological study, and at a time when many of the structural features of the cutaneous organs were poorly understood. Even the most recent investigation on the gorilla by Straus ('50) is based on skin obtained from embalmed specimens. None of the modern methods of histology and histochemistry has been used to study the skin of primates. Histochemical methods are particularly useful in the study of skin; it is possible, for example, to separate eccrine from apocrine sweat glands,

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even when they appear morphologically similar.

Our aim is to study the skin of all the major families, so that we may understand the principal attributes of the skin of all primates. These reports will appear as the animals are available to us, and will not necessarily follow any phylogenetic sequence. In general we have selected those techniques which have been most informative in the study of human skin. Although each of the papers which follows will have a brief coverage of the histochemical properties of the nerves, this aspect will be reported more extensively by Dr. Richard K. Winkelmann of the Mayo Clinic, who is primarily concerned with cutaneous innervation. Similarly, Dr. Herman B. Chase of Brown University will give, in time, a fuller report on the pilary system than is covered in these papers.

MATERIAL AND METHOD

This study is based upon 6 adult specimens, only two of which, one male and one female, were killed. The animals were in good health and in a good nutritional state. In the laboratory, the animals were fed a varied diet of fruit, cereal and meat. Bananas, grapes, ripe peaches, pears and apples were supplemented with a poultice of pablum and evaporated milk. For meat we used the better grades of canned dog food, and live young mice. The pieces of skin used in this study were removed while the animals were still alive, under deep nembutal anesthesia.

Pieces of skin were taken from every part of the body. For general histological studies, pieces of skin were fixed in Helly's fluid and 10% formalin and embedded in paraffin. Sections of these tissues were stained with Giemsa, with toluidin blue buffered to various pH values (Montagna et al., '51a), and treated with the PAS reaction for glycogen and saliva nondigestible carbohydrates. Phosphorylase and succinic dehydrogenase activities were demonstrated in frozen sections of unfixed tissues, using the methods of Takeuchi and Kuriaki ('55) and Farber and Louviere ('56). The following enzymes were studied in frozen sections of tissues fixed in chilled 10% formalin for 4 hours: alkaline phosphatase (Gomori, '52); acid phosphatase (Rutenburg and Seligman, '55); n cific esterases (Pearse, '53); tween ase, or lipase (Stowell and Lee, acetylcholinesterase and butyryl esterase (Montagna and Ellis, '57).

OBSERVATIONS

The potto, *Perodicticus potto*, (fig. longs to the following classification '53):

Order: Primate
  Grade A: Strepsirhini
    Suborder: Lorisoidea
      Family: Lorisidae

Pottos are small, slow-moving, noc animals which inhabit the tropical f of Africa (Hill, '53). They are 12 inches long, with a tail two-and-on to three inches long. Their fur is woolly, grayish and brown. Sparse, ish, coarse hairs protrude an inch or beyond the underfur of the cheeks, and scapular regions. The few, short sae are found only on the mystacial r

The neural spines of the last t three cervical and the first two th vertebrae, characteristically protrude to 5 millimeters above the surface skin and are covered with thimb glabrous, thickly cornified skin.

When the animal is clipped, the is mottled or pock-marked, particula the nape and infrascapular regions. skin of the sacral region is darker that elsewhere and is oily to the Over the scrotum and the vulva th face of the skin is broken by inters fissures which outline a mosaic of rh figures, the surface of which is c by short, dense, velvet-like hairs. pungent musky odor, characterist these animals, emanates from the gions.

Although Hill ('53) records onl pairs of nipples, males and females three pairs. The anterior nipples jus dial to the axilla are the largest; th terior abdominal nipples are very and could be overlooked in an uns animal.

Other than general observations external features, made mostly fo purpose of systematics (Sanderson, we know nothing about the skin of animals. Some aspects of the skin

resemble those of the skin of the Sisk, '57), the insectivores and carni- s (our own unpublished data).

Epidermis

ıe epidermis is relatively thin. It is ‹er in the face, scalp, nape and dorsum, elsewhere it consists of only two or e cells in thickness. A few dendritic nocytes, sown between the cells of the l layer, impart some melanin granules e cells of the malpighian layer. In the ıs and soles, numerous melanocytes found in the apices of the epidermal llae, crowded around the junction of ducts of sweat glands; the epidermis een adjacent papillae is free of me- cytes. In the skin of the tail, the epi- ıis is nonpigmented but many large lritic melanocytes are found in the ıis. In the skin of the scrotum, the ınocytes are very large, and their cell es bulge below the dermo-epidermal tion. Some melanocytes actually re- in the dermis, but their large dendritic esses extend up into the epidermis. er melanocytes farther down in the ıis also send processes toward the epi- ıis, but they may or may not make act with it. These are much larger the melanocytes found elsewhere in skin.

he epidermis has a barely distinguish- stratum granulosum, no stratum luci- , and a relatively thin stratum cor- n. Even in the palms and soles where epidermis is very thick, the stratum ulosum and the stratum lucidum are very distinct. The spiral canals of the at ducts distinctly traverse the very k stratum corneum. From the cells of basal layer everywhere, and particu- where the epidermis is thickest, cyto- mic processes are insinuated into the nis. Cells in mitosis, however, never ain basal processes. Mitosis is found in the basal layer. Intercellular ges between the cells are clear only in epidermis of the palms and soles.

thick "basement membrane," consist- of matted PAS-reactive fibers, particu- well-developed in places where the ermis is thickest, separates the epi- nis from the dermis.

The cells of the basal layer of the epidermis are strongly basophil, indicating a rich content of ribonucleic acid. The cells of the spinous layer show progressively less basophilia as they rise to the surface.

The epidermis is generally free of demonstrable glycogen. In the face and lips, glycogen may be found in the cells at the bottom of grooves and pits, where the process of keratinization seems to have been slowed down or stopped (Montagna et al., '51).

The epidermis everywhere has intense phosphorylase activity, limited to the cells of the malpighian layer. The reaction is most intense in the epidermis of the palms and soles, and elsewhere in the thicker epidermis of the head, the genital regions and the tail. The entire malpighian layer has strong succinic dehydrogenase activity. The reaction is strongest in the basal cells, where reactive granules are particularly numerous in the cytoplasm below the nucleus.

Although none of the epidermal cells contains alkaline phosphatase activity, large, dendritic cells scattered throughout the epidermis are characteristically rich in this enzyme. These cells have a perikaryon located between the basal cells and large, branching processes that reach as far as the stratum corneum (fig. 3). The cells resemble dendritic melanocytes, except that they are larger, and melanocytes show no phosphatase reaction. Phosphatase-rich dendritic cells are numerous around the junction of the epidermis with the pilary canals and are also found in the palms and soles. The upper layers of the epidermis, especially in the face and lips, have strong acid phosphatase activity; the basal cells are weakly reactive. In the palms and soles a heavy concentration of the enzyme is found in the epidermal papillae, but the epidermis between them has none. The upper part of the epidermis everywhere, and particularly the stratum corneum, contains lipase and esterases.

The apocrine glands

All of the sweat glands in the general body skin are of the apocrine type. Each gland grows near a hair follicle, but there is usually only one gland for each hair

group, regardless of the number of follicles the group contains (figs. 2 and 21). The glands are largest and the most numerous in the skin of the scrotum and vulva. The glands open by a narrow duct directly to the surface by a funnel-like dilatation near a pilary canal, but not inside it. Below the dilated orifice, the duct has a very narrow diameter and is composed of two layers of cuboidal cells, so flattened that in transverse sections the duct resembles an arteriole. The duct joins abruptly the thick secretory segment midway in the dermis (fig. 21). The secretory segment is slightly coiled and resides entirely within the dermis; in the skin of the face, the axilla, the tail, the scrotum and the vulva, where the glands are larger and more tortuous, they extend beyond the lower limit of the dermis into the subcutaneous fat.

The columnar cells lining the glands have a cuticular border. A mantle of large myoepithelial cells, aligned parallel to the long axis of the tubule, is between the base of the secretory cells and the thick basement membrane. The lumen of the larger glands is scalloped, some of the cells being taller than others; many of the larger cells have cytoplasmic nipples that extend into the lumen. Only some of the glands contain stainable colloid or visible cell debris in their lumina.

The secretory cells have an acidophil ground cytoplasm with coarse basophil bodies clustered below the nucleus; small basophil granules are found just above the nucleus. An area above the nucleus, and about the size of the nucleus, corresponds to the negative image of the Golgi apparatus and is largely achromic. Relatively coarse, lightly pigmented, basophil granules are clustered above this area. The luminal cytoplasm above the basophil granules is replete with delicate achromic granules.

With toluidin blue buffered to pH 5.0, only the nucleus and the coarse basophil bodies are stained, the rest of the cell remains unstained. With the dye buffered to pH 6.0, however, the granules in the superficial cytoplasm stain a deep metachromatic color. The colloid in some of the glands is also stained metachromatically.

In the larger glands of the face secretory cells have a diffuse PAS re ity which is digestible with saliva which must be glycogen. The myoepit cells may also contain some glycogen. glands elsewhere on the body rarely tain glycogen. The granules which metachromatically with toluidin blue fered to pH 6.0 are also PAS-positive saliva resistant (fig. 4). The colloid i lumen may also be PAS positive. In trast to the secretory cells, the cells c excretory ducts always contain glyc None of the glands contain demonst ionic iron.

In the secretory coils, granules rea for succinic dehydrogenase nearly fill cells, and are particularly numerous b and above the nucleus (fig. 9). The epithelial cells have only sparse reac The cells of the duct are weakly reac

The entire duct from the orifice to secretory coil has strong phosphor activity (fig. 5). The secretory segm however, contains either a trace of tivity or none; the myoepithelial cells very little enzyme (fig. 6). Alkaline p phatase is concentrated in the apical bo of the secretory cells (fig. 7). The re the cell and the myoepithelial cells ar most unreactive. The ducts show n action. The secretory cells abound in phosphatase; those of the duct have n The secretory coil is richer in tween e ases, (fig. 22). alpha and AS-ester than any other cutaneous structure duct has a minimal reaction. None o glands is surrounded by nerves which tain demonstrable cholinesterases.

The inguinal glands

Before describing the glands in thi gion, it is well to remember the pecu ities of its skin. The surface of the scro and vulva is broken by deep fissures. dritic melanocytes are found only in epidermis lining the crevices; that li the smooth surface facets is nonpigmen Clusters of fine hairs grow both on surface facets and in the crevices. L sebaceous glands accompany the foll of these hairs.

A solid bed of coiled glands ext through the whole dermis, passes thro

:unica dartos, and reaches the hypo-
iis (fig. 8). The glandular field in the
um is about two centimeters in diam-
and one-half centimeter in thickness;
in the vulva is smaller. These *scent
ls* are comparable to the brown in-
al glands of the rabbit (Montagna,
The glands in the inguinal region
armosets (Wislocki, '30) are different
will be described in detail in a future
r.

guinal glands are composed of indi-
al, coiled, simple, tubular glands
e ducts rise straight up to the surface
open into pilary canals at the deepest
of the crevices (fig. 9). These orifices
ilated into elliptical receptacles which
lly contain concretions of secreted
rial. Adjacent glands are separated
l-defined connective tissue partitions.
secretory coils measure from one-
ter to one-half millimeter in diameter,
terminate abruptly into a narrow duct
t 50 μ thick. A thick, hyalin basement
brane surrounds the glands. The
ls, clearly of the apocrine type, are
with tall columnar or cuboidal cells,
ree border of which often protrudes
lingual process into the lumen. The
elium rests upon a layer of large myo-
elial cells. The duct, similar to that
ie glands elsewhere on the body, is
oosed of two layers of flat cuboidal

ie secretory epithelial cells are similar
ose of the sweat glands over the rest
e body surface. They have a spherical
eus (often two) with one or more
eoli. The cytoplasm is replete with
ate, evenly distributed basophil gran-
and large mitochondria, so closely
ed that they are often aligned on the
axis of the cells.

ie cells of the duct abound in glycogen,
e of the secretory coil contain dust-
glycogen granules, and small, pig-
ted, barely PAS-reactive saliva resis-
granules. The content of the lumen
AS reactive and saliva resistant.

ie ducts have strong phosphorylase
ity from the pilary canal to the secre-
coil, but the secretory coils contain
; the myoepithelial cells have some re-
e granules (figs. 5 and 6). The entire gland is conspicuously reactive for succinic dehydrogenase. Alkaline phosphatase reaction is present only in the apical part of the secretory cells; the ducts show no reaction. The secretory tubules have an intense acid phosphatase reaction, but the ducts have none. The secretory coils, but not the ducts, have intense esterase and lipase activity. The inguinal glands resemble the apocrine glands in the skin of the general body surface in nearly all respects. The inguinal glands, however, have one unexpected difference; they are surrounded by a rich nerve plexus which contains abundant acetylcholinesterase. These nerves have no butyrylcholinesterase.

The glands of the volar side of the hands and feet

The palms, soles and digital pads contain eccrine sweat glands. The ducts of these glands open to the surface of the thick epidermis through coiled channels. The straight dermal part of the duct is very thin, about 20 to 25 μ in diameter, like that of apocrine glands, and is composed of two layers of squamous cells. The luminal cells have a barely differentiated cuticular border. Before they join the bottom of the epidermal ridges, the ducts become multilayered and the lumen funnels out in a wider coiled channel. In the intraepidermal part, the duct has a cuticular border composed of two or three cells.

The coiled secretory segment of the glands is thick and becomes abruptly constricted at the junction with the narrow duct, as in apocrine glands; therefore, none of the glomerate portion of the gland is composed of duct. The gland is lined with large pyriform cells differentiated into clear and dark cells (Montagna, '56). The larger *clear cells* have a spherical, finely stippled nucleus, and a cytoplasm with sparse, delicate granules barely stainable with basic dyes (fig. 10). The smaller *dark cells* seem to be piled up toward the lumen, often above the clear cells, in such a way that the epithelium appears to have two layers. The cytoplasm of dark cells contains basophil granules and some granules that stain metachromatically with toluidin blue. The nuclei are dense, never spherical, usually oval, and often mis-

shapen. The smaller dark cells are more numerous than the clear cells.

Duct and gland contain abundant glycogen (fig. 11). Small amounts of PAS-positive, saliva resistant material are found at the tips of the dark cells only. The lumen contains small granules of glycogen and a weakly PAS-positive, saliva resistant colloid.

Ducts and glands contain so much amylo-1,6-glucosidase and phosphorylase that a strong reaction is obtained by leaving tissues in the incubating medium only 5 minutes; in contrast, the epidermis, which is also reactive, requires a much longer period of incubation to show a reaction. In the intraepidermal part of the duct, only the luminal cells have phosphorylase reaction. The entire gland is also intensely reactive for succinic dehydrogenase. The glands contain small amounts of alkaline and acid phosphatases and traces of esterases.

In sections incubated with acetylthiocholine for the demonstration of cholinesterases, a reaction is obtained in the stratum corneum in the bottom of the sulci of the surface epidermis. The round, tactile corpuscles of Meissner are intensely reactive (fig. 12). The knotted nerves that emerge at the base of these corpuscles also contain acetylcholinesterase but their distal path does not. Each epidermal ridge is surrounded by a nerve net supplied by branches which converge toward the nerve fibers from the tactile corpuscles. All of these nerves are moderately reactive for acetylcholinesterase. All small arteries and arterioles are supplied by reactive nerves. Although the ducts of the glands have no demonstrable nerves around them, the entire glomerate portion of the glands is enveloped by an intensely reactive plexus of large nerve fibers (fig. 13). When eserine is added to the incubation medium all of the reactions in the nerves is abolished, that in the Meissner corpuscles is not. When butyrylthiocholine is used as a substrate, only the tactile corpuscles are reactive.

The pilary system

Hair follicles grow in crowded groups of 4 to 20, separated from each other by swirling connective tissue fibers (figs. 14
15). The hairs from each group of fo
emerge to the surface in depressions w
correspond to the pock-marks visib
the surface of the shaved skin. Hair g
are closer together in the dorsal an
tensor regions than they are in the ve
and flexor regions.

Only some of the follicles in these is
of hair follicles share a pilary canal;
of them open singly to the surface.
majority of the follicles in a hair grou
approximately of the same size, but
of them may be larger. In the scalp
back, where the pelage is coarser, the
follicles are more numerous than
where. Even though the follicles in
group grow very close together, they
dischronous phases of growth; som
licles may be active while adjacent
are quiescent (fig. 15).

Each follicle has a long pilary
with one or two small sebaceous g
opening at the bottom of it. The
canal is encircled by giant dendritic
strongly reactive for alkaline phospha
identical with those in the surface
dermis (fig. 3). Recognizable melano
not reactive for alkaline phosphatase
also found in the wall of the pilary c

The hair follicles resemble those o
dents and lagomorphs. Active follicle
very long and narrow with the bulb
ing in the subcutaneous fat. In rela
thin skin the lower part of the follic
the hypodermis is bent against the
niculus carnosus as in the skin of ro
(fig. 2). The elongated bulb enclo
narrow and long dermal papilla. Me
cytes are clustered at the top of the
and rarely descend to the sides of it.
hair follicles are surrounded by a
thick, glassy membrane. Hairs em
fully-formed just above the constri
of the bulb; they can be medullated o
depending on their thickness and the
dulla is usually interrupted by air
In each medulla cell, the cytoplasm is
mented in the upper part, but the l
part which contains the nucleus is
In coarse, medullated hairs the cort
pigmented, but in finer ones only
medulla cells contain melanin; the f
hairs with no medulla have no pigme

iescent follicles are less than one- the length of active ones. The igmented, elongated club hair they in is similar to that of rodents and ivores. Whether or not the hair is pigted or medullated, the shaft of the hair e the club is always nonmedullated nonpigmented for a distance above the ice of the skin. This means that bea follicle becomes quiescent, the folng sequences of events take place; first ases to form a medulla and its melanobecome inactive, then a club is ed. The hair club is surrounded by an elial capsule which is rarely thicker two layers of cells. The cells of the elial capsule are large and rounded the outer wall is pebbled; in transverse ons the outer side of the capsule is oped. Below the club, the epithelial ule is continuous with the hair germ e shape of an inverted cone. The hair i is in contact with the ball-like free ial papilla (fig. 20). Occasional denc pigmented cells can be seen between ells of the hair germ.

ie club is formed a considerable dise above the bulb, in the region that coronds to the keratogenous zone (figs. .7 and 18). The epithelial capsule and of the hair germ are formed from the of the outer root sheath; the bulb and of the outer root sheath below this on degenerate. During this process the ei of the bulb undergo karolytic iges and the cytoplasm becomes igly acidophil. In catagen, then, the largely or entirely degenerates and epithelial capsule and the hair germ are ied from the cells of the outer root th above the level of the bulb (Mona and Chase, '56).

air follicles are practically avascular. some of the larger, active follicles a few capillary loops partially oped around the lower part, but there never networks around the bulbs, and dermal papillae are avascular.

ll hair follicles, active or quiescent, ain glycogen. In active follicles, glycois restricted to the cells of the outer ith, extending from the wall of the ry canal, which contains none, to the of the bulb. The cells of the epithelial sac and those of the hair germ of quiescent follicles also contain glycogen (fig. 18). This is singularly different from the quiescent follicles in all nonprimates we have studied, none of which contains glycogen.

All follicles are very rich in phosphorylase activity. Enzyme activity is as abundant in quiescent as it is in active follicles (figs. 15 and 16).

The dermal papilla of either quiescent or active follicles contains alkaline phosphatase. In active follicles enzyme activity is also found in the cells of the outer sheath around the lower third of the follicle. The wall of the pilary canal also contains some enzyme activity. The large, phosphatase-rich dendritic cells described earlier in the epidermis encircle the pilary canals (fig. 3); the melanocytes in the upper bulb of the follicles are not reactive. The entire cellular structure of the follicles is reactive for acid phosphatase.

In quiescent follicles tween esterase activity is concentrated throughout the epithelial capsule and hair germ, and is particularly strong in the pilary canal, just from above the club, at the entrance of the sebaceous ducts (fig. 21). In active follicles the enzyme is concentrated in the outer root sheath and in the lower part of the pilary canal, where the inner root sheath disappears. The distribution of nonspecific esterases in hair follicles is essentially similar to that of lipase, the greatest concentration of which is in the pilary canal, where the inner root sheath disappears.

The sebaceous glands

Most of the sebaceous glands are relatively small, have no duct, and open directly into the pilary canal. The orifice of the gland has a collar of undifferentiated cells that blends imperceptibly with the cells of the pilary canal. In the face, the scalp and the scrotum, the glands are larger than those elsewhere in the body and they have a duct.

The cytoplasm of the undifferentiated sebaceous cells is rich in ribonucleic acid. During early sebaceous transformation, very small lipid globules first appear around the nucleus. These lipid droplets increase in number and in size, the cells become

larger, and the cytoplasmic basophil bodies become scattered between the droplets. The mature sebaceous cells still have distinct basophil bodies stranded between the large lipid globules (Montagna, '56). When stained with toluidin blue buffered from pH 5.0 to 6.0, the cytoplasm of the undifferentiated cells shows a delicate metachromatic staining, probably indicating the presence of mucopolysaccharide. The ground substance in the loose connective tissue around the glands is always stained a strong metachromatic color. During differentiation, the lipid droplets increase in size as the cells become larger; lipid droplets coalesce and the cells break up to form sebum. Sebaceous transformation is very gradual and sebum is usually found only at the entrance of the gland into the pilary canal. The fundus of the glands rarely contains formed sebum.

The nuclei of the undifferentiated cells are intensely basophil and Feulgen reactive, and contain at least one large nucleolus. In nearly mature cells, the nucleus shrinks, and the Feulgen reactivity gradually fades. It remains deeply basophil, however, even when stained with toluidin blue buffered to pH 4.5.

When a duct is present, its cells contain demonstrable glycogen. In the gland proper, glycogen is found only in those of the face, lips, brow and scalp (fig. 22); elsewhere, the glands contain none. This is a regional difference. In the glands of the head, glycogen has an inverse relation to the degree of differentiation of the cells.

The short duct is strongly reactive for phosphorylase, but only the glands on the head and on the scrotum show appreciable enzyme activity; those over the rest of the body show little activity. The enzyme is concentrated in the undifferentiated cells at the periphery of the fundus and gradually fades during sebaceous transformation (fig. 23).

The undifferentiated sebaceous cells and the cells of the ducts show strong succinic dehydrogenase activity. Sebaceous glands have no alkaline phosphatase and only traces of acid phosphatase.

In contrast with all other cutaneous structures, the sebaceous glands have a faint, diffuse, tween esterase activity. AS esterase, however, is abundant throu the glands, and in the sebum; in esterase is concentrated in the glan cells but not in the sebum. All seba glands show intense alpha esterase tion, but the sebum is unreactive.

The dermis

The thick dermis consists almos tirely of a fibrous reticular layer (fig The papillary layer is only 10 to 20 thickness; it contains a few fibroblasts nuclei flattened parallel to the surfa few thin collagenous fibers, and a sc population of reticular fibers. This la so thin that in many places the epide seems to be resting directly upon the ular layer. Since there is practicall papillary layer, a vascular plexus, suc that found in man (Montagna and '57a) and in higher primates is also ab

The reticular layer is thickest in scalp, nape and back, and thinnest on ventral surfaces of the body. The po tion of fibroblasts between the collage fibers is remarkably scanty. The pi baceous systems and sweat glands ar veloped by loose connective tissue delicate fibers, rich in cells and wi scanty supply of blood vessels; they ar in contact with the fibrous reticular l This connective tissue is characteristi like a true papillary body. The blood sels that traverse the dermis are also rounded by a bed of loose areolar tis This areolar tissue contains many cells mostly in the shape of fibrobl some of them are rounded and replete granules. The mast granules are well served in Helly-fixed tissues; they are positive, stain metachromatically with idin blue buffered to any pH level and tain esterases and phosphatases. cells are never found any distance f blood vessels.

A few, delicate elastic fibers are loo interlaced with the collagenous fi They are more numerous around hair licles and sweat glands, and are practic absent underneath the epidermis.

Some small, dendritic cells, found mo around hair follicles, contain pigment the skin of the scrotum and of the however, large dendritic dermal mel

are scattered around the hair follicles sebaceous glands.

the scrotum, a thick, discontinuous of smooth muscle traverses the dermis the bed of glands. This muscle is osed of two layers of fibers oriented ht angles to each other. To a limited t, the same features described in the um are found in the labia of the le.

e dermis of the scrotum contains nu-us nerve fibers which contain acetyl-nesterase. Nerve fibers encircle the le fibers; many rise up to the papillary some invade the epidermis, and s are attached to rounded sensory ngs which may be genital corpuscles. sensory corpuscles and the muscle are also reactive for butyrylthiocho- the nerves are not. The dermis is rlain by a nearly continuous pannicu-arnosus. This is thicker on the dorsal on the ventral surface.

DISCUSSION

e skin of the potto is relatively primi- The simple epidermis has practically ratum granulosum. The thick dermis a very thin papillary body, and con- very few capillaries, and most of the neous appendages have a scanty blood ly. The thin, very long hair follicles uce hairs which resemble those of nts and insectivores. Hair follicles in large clusters or islands, between h the skin is glabrous; this pattern s to bridge the gap between the pelage dents, bats and insectivores, in which ndividual follicles grow evenly spaced, that of most other mammals in which groups are composed of fewer and conjoined follicles.

all mammals we have studied pre-sly, the outer root sheath of active les is always laden with glycogen, but the quiescent follicles of man contain gen. The quiescent follicles of the , then, with their rich content of glyco-are singularly different from those of rimate mammals. Also, quiescent fol-s, like those of man and unlike those onprimates, abound in phosphorylase. e sebaceous glands are small, usually no duct and resemble those in the of rodents. In the face and near the genital regions, the glands are larger and have a duct. It is surprising to find glycogen in the glands of the head since we have not found this substance in sebaceous glands other than in those of man (Montagna, '56). This difference recalls another regional difference in the distribution of phosphorylase. Although the undifferentiated cells in all glands have some phosphorylase, only the glands in the head and the genital regions abound in the enzyme. This is curious since of these, only the glands on the head contain glycogen.

The dendritic, alkaline phosphatase-rich cells found in the epidermis and in the pilary canals have not been demonstrated with other techniques. They resemble the dendritic melanocytes, but they contain no melanin, and the recognizable melanocytes are not reactive for phosphatase. The significance of these cells is unknown. They have not been found in other lorisoids we have studied so far.

In man, sharp distinction can be made between apocrine and eccrine sweat glands on histochemical grounds. Apocrine glands rarely contain glycogen, they are lacking in phosphorylase, are low in succinic dehydrogenase, and with one possible exception, the glands of Moll, are never surrounded by cholinergic nerve fibers. Eccrine sweat glands abound in glycogen, phosphorylase and succinic dehydrogenase activity, and are always wrapped with nerve fibers containing cholinesterase. The sweat glands of the potto have all the histological and histochemical attributes of apocrine glands, except that they may contain some glycogen. Thus, the apocrine glands of the potto may be considered less specialized than those of man. If eccrine and apocrine glands have a common ancestoral origin, the primitive type probably contained glycogen. Although none of the apocrine glands of the general body surface are surrounded with nerves which contain cholinesterase, the inguinal glands, which are identical in most respects with the other apocrine glands, are invested with numerous nerves rich in cholinesterase. These large glands are highly specialized structures, with special adaptive significance, probably related to the reproductive activities of the animal. Studies on the

skin of other primates, to be published later, show that this particular specialization of the apocrine glands is not unique to the potto.

The sweat glands in the volar side of the hands and feet resemble both eccrine and apocrine glands. Although they open to the surface through helicoid channels in the epidermis, their duct is very narrow, and the glomerate secretory part is so wide that the transition between secretory segment and duct is as abrupt as it is in apocrine glands. Thus, all of the glomerate part consists of secretory segments and there are no coiled portions of the duct. This is in contrast with the eccrine glands of man, in which the diameter of the duct is as wide as that of the secretory coil, and about one-third of the glomerate part of the gland consists of coiled duct. The eccrine glands are composed of dark and clear cells as are those of man, but the cells, unlike those of man, contain relatively large secretion granules. The glands are well supplied with cholinergic nerves, as all known eccrine glands are. The eccrine glands of the potto, then, seem to have departed very little from a hypothetical ancestral type, and their structural and functional attributes resemble both types of glands.

After studying the distribution of phosphorylases in the skin of man and in that of several laboratory mammals, Ellis and Montagna ('58) suggested that the presence of this enzyme is characteristic of human skin, the other mammals having practically none. The skin of the potto, however, contains even greater concentrations of it than human skin does. All of the various primates we have studied (to be reported later) also show abundant enzyme activity. It must be concluded, then, that abundant phosphorylase in skin is a characteristic feature of primates and not simply of man. This fact begins to call attention to histochemistry as yet another tool which can be used in the study of anthropology.

SUMMARY

1. The relatively thin epidermis contains few dendritic melanocytes; in the tail region, dermal dendritic melanocytes send processes up into the epidermis to impart melanin to it. Large, dendritic cells, demonstrated only with the techniqu[e] alkaline phosphatase reside in the dermis. The epidermis contains sever[al en]zymes, among them phosphorylase.

2. The hairs of the potto are simil[ar to] those of rodents. The long, narrow [fol]licles grow in large islands, between w[hich] the skin is glabrous. Both growing [and] quiescent follicles abound in glycogen [and] phosphorylase activity; these subst[ances] are not found in the quiescent follicl[es of] nonprimates we have studied.

3. The sebaceous glands are gener[ally] small. The glands in the head contai[n gly]cogen; those elsewhere do not. Hereto[fore] we had encountered glycogen only in [the] sebaceous glands of man.

4. Pottos have one or two sweat gl[ands] associated with each hair group. Th[ese] glands have the characteristic featur[es of] apocrine glands.

5. The skin of the scrotum and [the] vulva contains rich fields of apo[crine] glands, larger, but otherwise simila[r to] those over the body surface. The sin[gular] peculiarity of these glands is that the[y are] surrounded by nerves rich in acetylch[olin]esterase.

6. The sweat glands on the volar [side] of the hands and feet share the fea[tures] of both eccrine and apocrine glands. [They] are perhaps very primitive eccrine gl[ands].

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PLATES

PLATE 1

EXPLANATION OF FIGURES

1 An adult male potto. Observe the long, sparse guard hairs, particularly over the head which protrude beyond the thick, woolly underhair.

PLATE 2

EXPLANATION OF FIGURES

2 General view of the skin showing some of its features. The thin epidermis (curved arrow) is only about two cells in thickness. The skin has practically no papillary body and the reticular layer is fibrous and very thick. Contrast the length of the growing hair follicles (heavy, short arrow) with the quiescent ones in the upper part of the figure.

3 Phosphatase rich dendritic cells in the epidermis (indicated by bracket) and around the pilary canals.

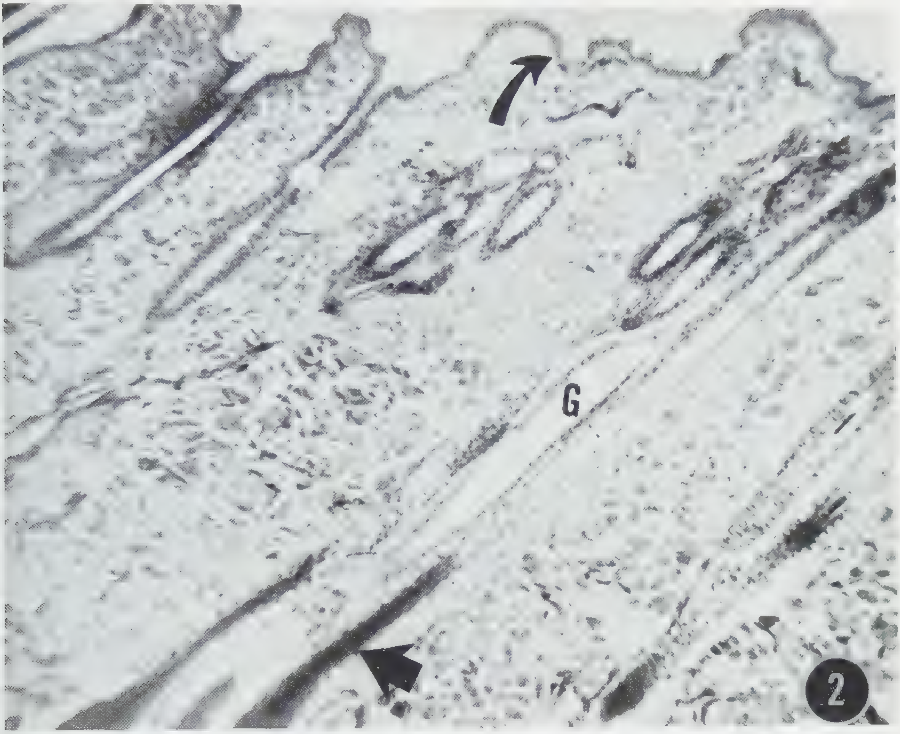
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PLATE 3

EXPLANATION OF FIGURES

4 Cross sections of apocrine sweat glands from the face showing numerous PAS-reactiv granules. This is not glycogen.

5 Strongly phosphorylase reactive duct of an apocrine sweat gland. The reaction stop abruptly at the transition of the duct and the secretory segment (arrow).

6 Phosphorylase reaction in the myoepithelial cells of the apocrine glands in th inguinal region; the epithelial cells are unreactive.

7 Strong alkaline phosphatase activity in the apical border of the cells of the apocrin glands from the lumbar region.

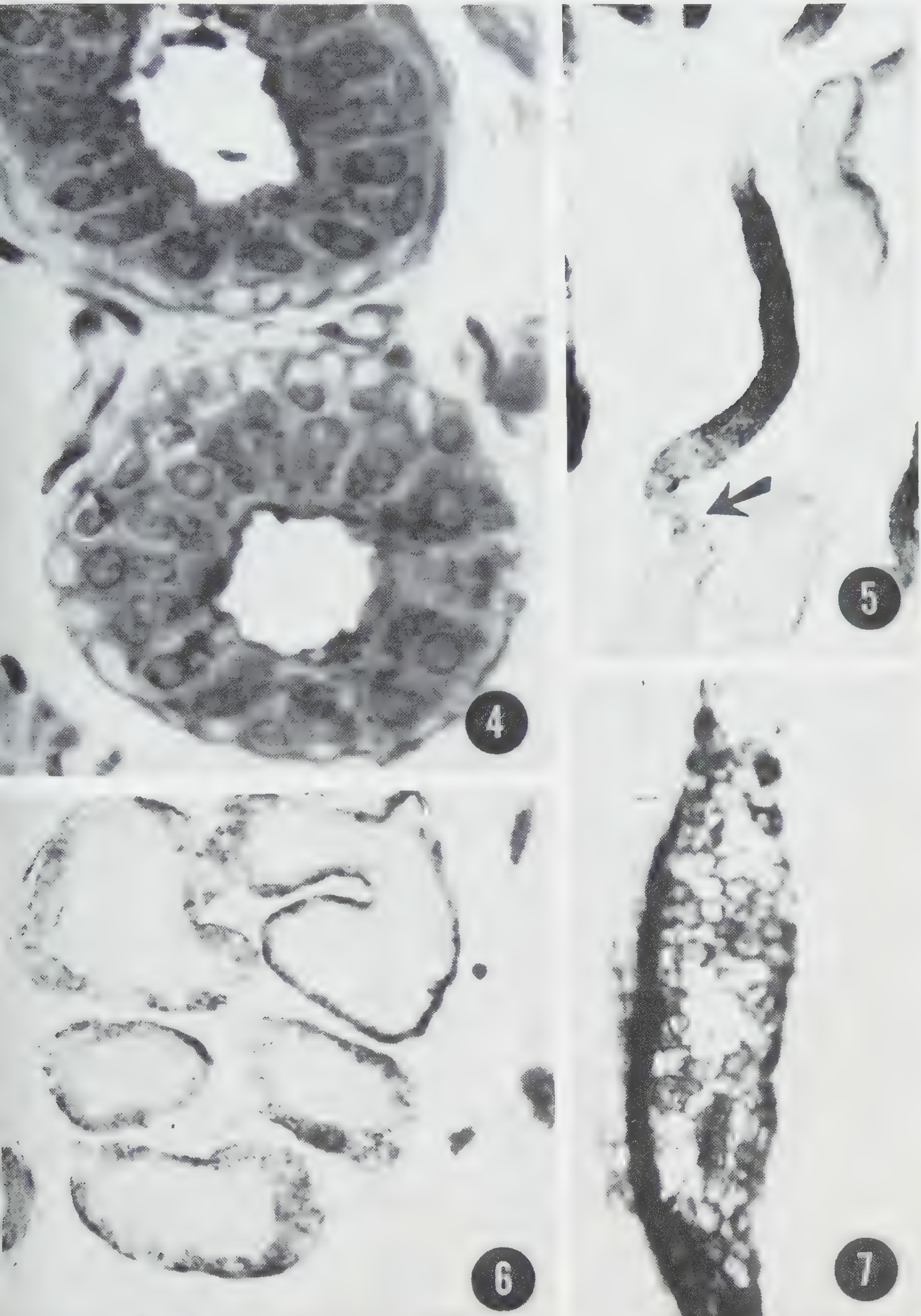
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PLATE 4

EXPLANATION OF FIGURES

8 Small section of the inguinal glands showing several glands cut at various planes.

9 Strong succinic dehydrogenase activity in the secretory segments of the inguinal glands.

10 Gland from the volar side of the palm showing clear and dark cells. The straight arrow points to the nucleus of a clear cell; the curved to the nucleus of a dark cell. Stained with toluidin blue buffered to pH 4.5.

11 Glycogen in the cell on the volar side of the palm, largely concentrated in the dark cells.

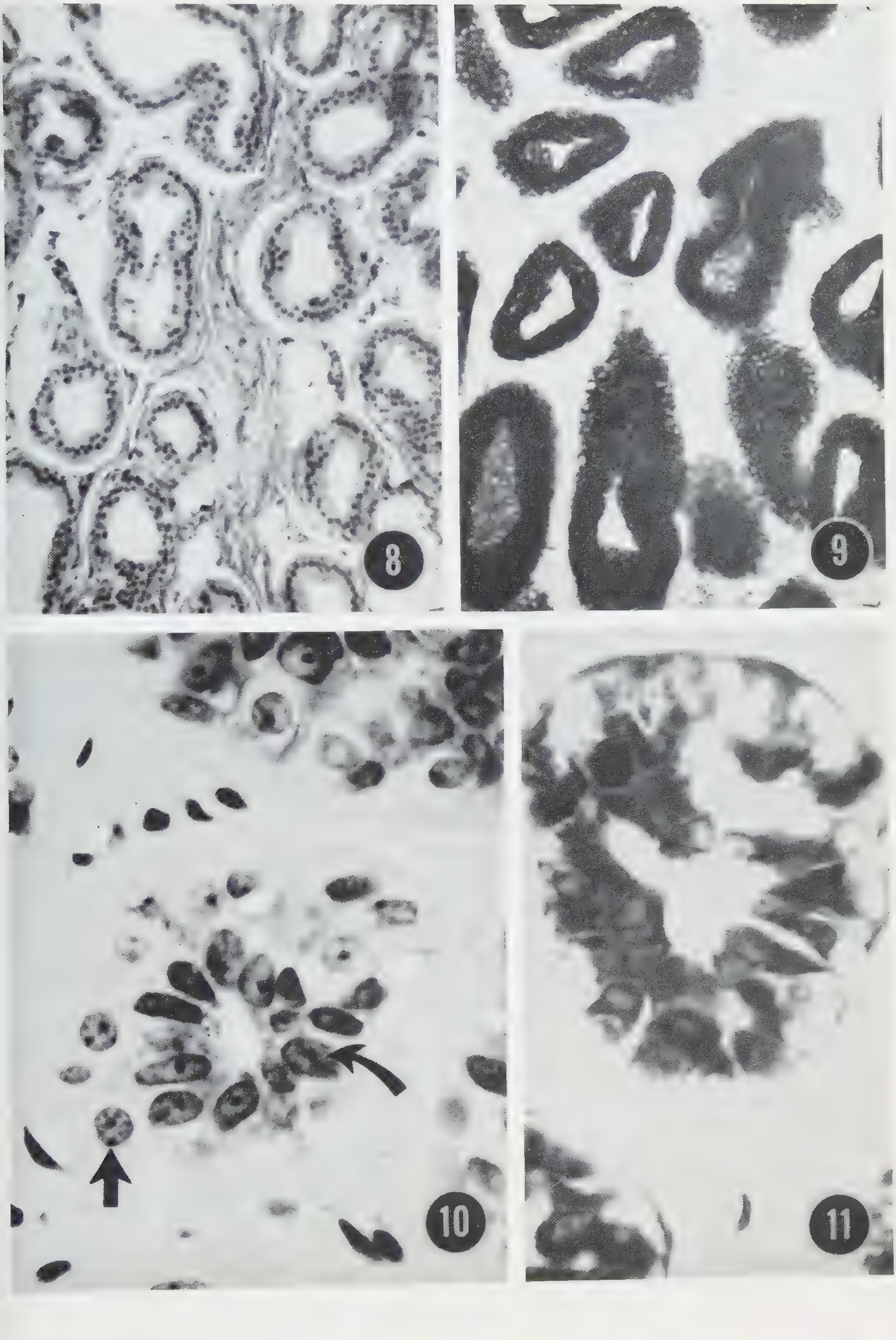
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PLATE 5

EXPLANATION OF FIGURES

12 Cholinesterase in the corpuscles of Meissner (arrow) and in nearly all other cutaneous nerves.

13 Cholinesterase-rich nerves around the glands on the volar side of the palm.

14 Surface cut of the skin showing a hair group. Arrow points to an apocrine gland. Section treated with the technique for succinic dehydrogenase.

15 Phosphorylase activity in the follicles of two adjacent hair groups. Arrows point to active follicles; most of the other follicles are quiescent. Both active and quiescent follicles are rich in phosphorylase activity.

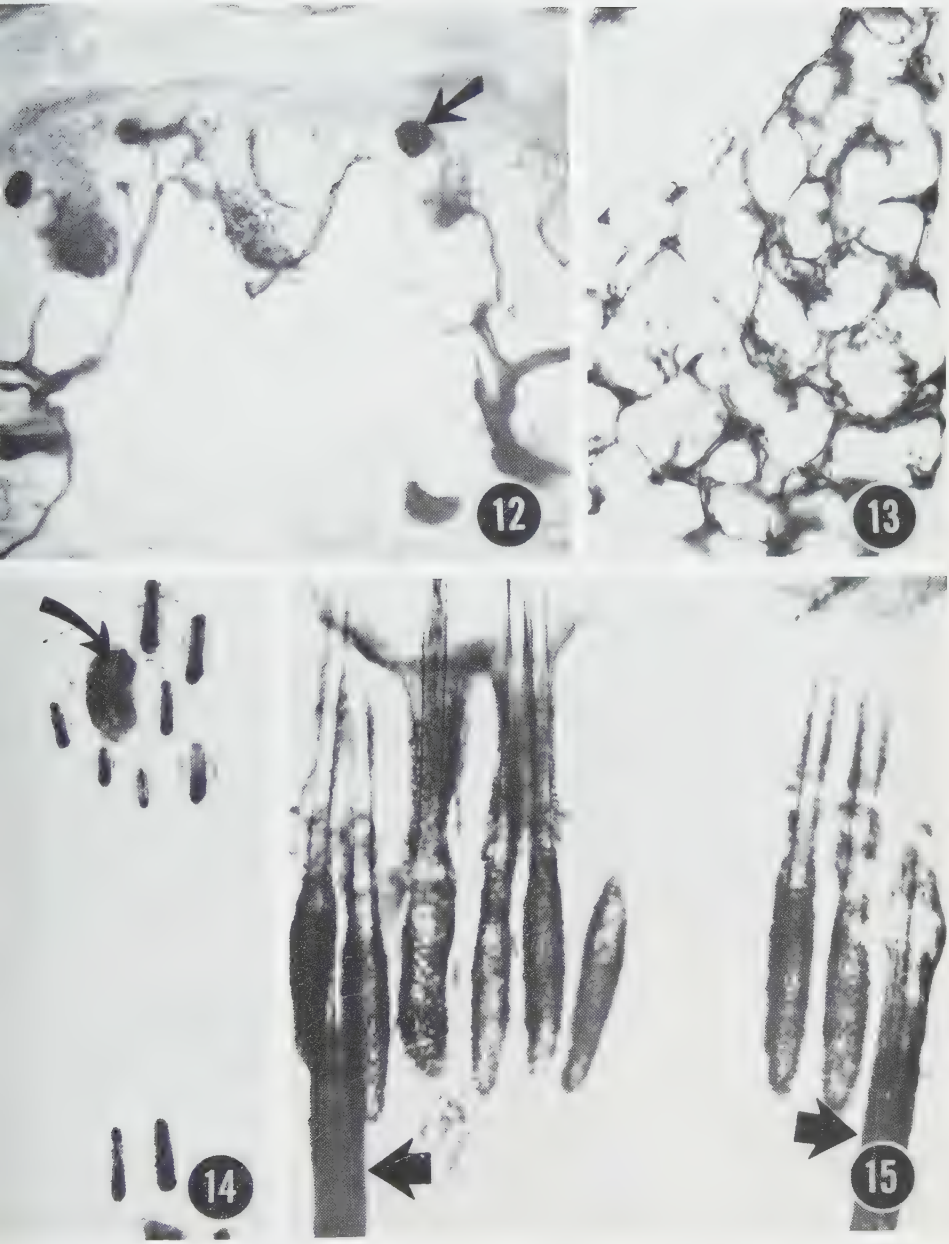
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PLATE 6

EXPLANATION OF FIGURES

16 Phosphorylase activity in a hair follicle during catagen. The hair club has formed a long distance above the base of the follicle. The follicle below the club is degenerating.

17 and 18 Two sections of the same follicle in catagen, showing the formation of the club; the follicle below the club is degenerating. The arrow points to an apocrine sweat gland.

19 Glycogen in the epithelial capsule of two quiescent hair follicles. Treated with the PAS reaction.

20 Enlarged detail of figure 18, showing the "hair germ" and the dermal papilla (arrow).

21 Transverse section through a quiescent follicle showing the club hair and epithelial capsule, laden with glycogen.

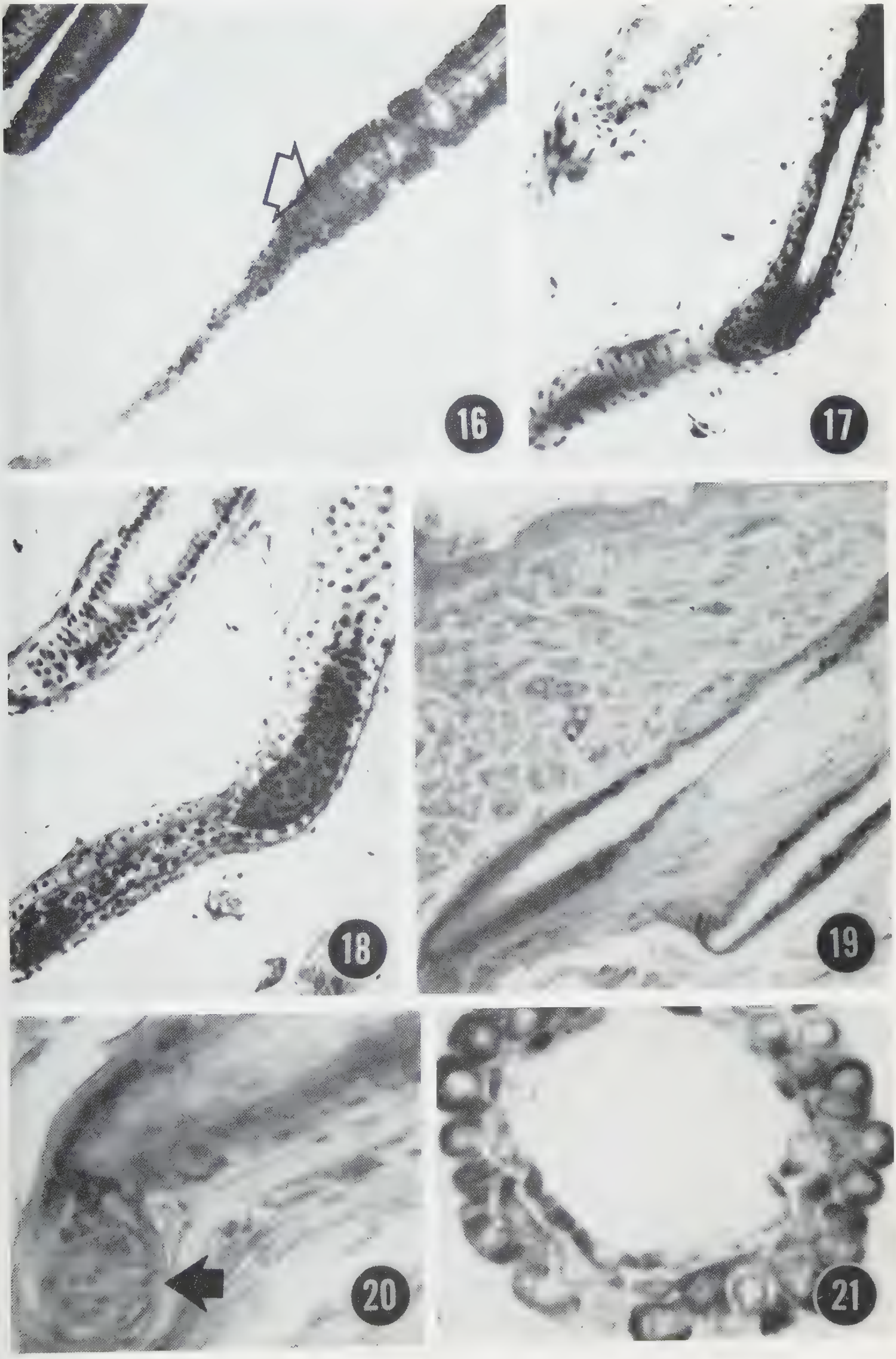
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PLATE 7

EXPLANATION OF FIGURES

22 Tween esterase activity in hair follicles and in an apocrine sweat gland. Arrow points to the transition between the duct and the secretory part of the gland.

23 Glycogen in the undifferentiated and partially differentiated cells of the sebaceous glands of the face. The fully differentiated cells are free of glycogen.

24 Phosphorylase activity in the sebaceous glands from the scrotum.


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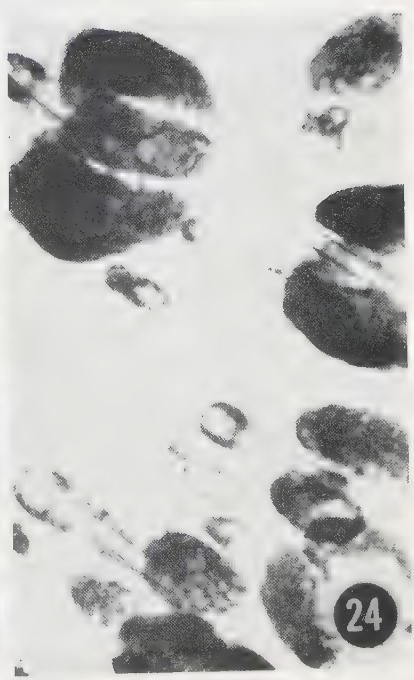
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HENRI VICTOR VALLOIS

Viking Fund Medalist
for 1958

HENRI VICTOR VALLOIS

ing Fund Medalist for 1958

e great musician, Fritz Kreisler, was yn in his prime as a violinist's violin- This supreme form of tribute has been rded Professor Henri Victor Vallois ugh the many recognitions he has ved for his work in anatomy and phy- anthropology in France during his er of nearly half a century. The value e products of his labors and the in- tion of his personality and outlook moved the American Association of ical Anthropologists to salute him n tonight as the 1958 Viking Fund alist in physical anthropology.

. Vallois is professor of the Mu- n national d'Histoire naturelle and tor of the Musée de l'Homme in s. He became a licentiate in sci- from Montpellier in 1910 and re- d the doctorate in medicine from same institution in 1914. The ersity of Paris conferred upon him degree of doctor of natural science 921 and he was awarded an honorary orate by the University of Mayence in . He joined the faculty of medicine e University of Toulouse in 1920 and ed as its professor of anatomy from to 1940. At Toulouse he was also tor of the laboratory of anthropology e Ecole pratique des Hautes Etudes held a similar post at the University aris in 1937. In 1938 he became pro- r and in 1942 director of the Institut aléontologie humaine. He was made ofessor in the Ecole d'Anthropologie in s in 1945 and since 1949 has been in ge of instruction in anthropology on Faculty of Sciences of the University aris.

. Vallois has served in strategic posi- in every important international and onal congress or conference related to ical anthropology during his career. In 1934 he was secretary and later president of the International Committee for Standardization of Anthropological Techniques.

He was awarded the Croix de Guerre during World War I and became a Chevalier of the Legion of Honor in 1933 and an Officier in 1957. The Royal Anthropological Institute awarded him the Huxley Memorial Medal in 1951. He has been on 13 scientific missions to foreign parts which have included nearly every country in the world and has been a representative participant in additional international conferences.

Dr. Vallois' scientific publications include 295 titles, which may be roughly classified under 11 separate headings, namely: comparative vertebrate anatomy, comparative primate anatomy, human anatomy, anthropological anatomy, human origins, fossil man, the races of man, the anthropology of France, the anthropology of the Far East, the races of the French Empire and textbook and periodical writings. Twelve well known scientists have completed their doctoral theses in medicine or in science under his direction. Such breadth and depth of background easily justify reference to him as the "compleat physical anthropologist." Those who have had the privilege of visiting the Musée de l'Homme are familiar with the richness of its collections and the hospitality of its director.

Our honoree's achievements stand in a great tradition among his countrymen. Names like Daubenton, Lamarck, Cuvier, Broca, Topinard, Manouvrier and Anthony immediately come to mind. When Broca formed the Société' d'Anthropologie in Paris in 1859, he established physical anthropology as a separate branch of science, the centennial of which the A.A.P.A. will cele-

brate at its annual meetings this year. It is not possible to enumerate all the French scientists whose contributions have subsequently enriched our field. We mention only that Dr. Aleš Hrdlička, the founder of the American Association of Physical Anthropologists and of its Journal, studied with Manouvrier and remained throughout his distinguished career of leadership and contributions, strongly influenced by the French school of anthropologists. Our Association is thus happily able to acknowledge a special kinship with Professor Vallois.

Since among scientists there are no boundaries of geography, nationality, culture or descent, it seemed an appropriate token of fellowship for our Associatio present its citation of Dr. Vallois in language rather than ours. Hence the lowing expression of our sentiments:

> The American Association of Physical Anthropologists, avec son estime et ses meilleurs souhaits, a l'honneur de proposer le Professeur Henri Victor VALLOIS pour la medaille Viking Fund d'anthropologie physique pour l'année 1958, en reconnaissance de son influence continuelle et prolongée en anthropologie physique en France ainsi que pour ses travaux scientifiques et administratifs. La bonne chance pour toute la vie!

W. MONTAGUE COBB, *Presi*
American Association of Physical Anthropolo
— for the Associa

Read at the Thirteenth Annual Dinner of the Wenner-Gren Foundation for Anthropological Research for the presentation of Viking Fund Medals and Awards, Hotel Plaza, New York City, March 6, 1959.

e Changing Pattern of Dentine Exposure in Human th Attrition

THOMAS MURPHY[1]
Department of Anatomy, University of Adelaide, South Australia

om the Piltdown anticlimax arise the tions: What *is* the human pattern entine exposure in occlusal tooth at- n? How may it be distinguished from of non-human primates, and from ar- al abrasion, fraudulent or otherwise? the Piltdown jaw Weiner and Oak- '54) state " . . . there appeared to be a single feature of the jaw and den- which could not be said to be defi- y ape-like, namely, the wear of the rs and canine." (cf. fig. 1C). In the detailed anatomical study of the own teeth Le Gros Clark ('55) pre- cumulative evidence for artificial sion which must be regarded as con- ve.

e criteria for natural wear, however, in largely subjective. The cited litera- lacks any reference to an independent tive description. If the pattern of wear is to be elevated to the status taxonomic criterion, such a descrip- is desirable.

a first step in providing answers to opening questions the present study ds the changing pattern of dentine sure in each permanent tooth with asing tooth attrition, as observed in ustralian aboriginal skull collection. cceeding study will deal with the de- of difference in dentine exposure een the molar teeth in each jaw, and een corresponding molars of upper lower jaws.

MATERIAL AND METHODS

ta were recorded from the large col- n of Australian aboriginal skulls ed in the Department of Anatomy, ersity of Adelaide, and in the South alian Museum.

preliminary review confirmed Camp- ('25) observation that, with regard trition, right and left sides are largely mirror images of one another. Accord- ingly records were taken only from the left side, and this side is illustrated through- out to facilitate comparisons.

Tooth arch terminology

In the anatomical position maxillary and mandibular occlusal surfaces are in apposition and must be "opened out" and straightened for descriptive purposes (fig. 1A). This provides the least ambiguous terminology, and one which is widely ac- cepted. It means, however, that the side of the maxillary teeth facing the top of the page is the buccal, while that of the mandibular teeth is the lingual. To avoid possible confusion the orientation is clear- ly sign-posted in each illustration.

Modal forms and variants

Records were taken from all teeth avail- able in situ without selection of skulls. Thus both sexes and all age groups are included.

While antemortem tooth loss in the ma- terial was negligible, an appreciable num- ber of teeth had become lost from the dried sockets. Nevertheless the lowest total incidence was 192, for the maxillary cen- tral incisor. The numbers thus appear sufficient to provide a valid study.

Teeth with no exposure of dentine are labeled in the illustrations with the capital letter N. The various patterns of dentine exposure in the others were classified and the incidence of each determined. From this information it was possible to sort out commonly occurring forms from variants.

The modal forms are labeled with a lower case lettering prefix (e.g.: a, b, c) and are arrayed as the top row of each illustration. In a few instances two dif- ferent forms had an almost equal repre-

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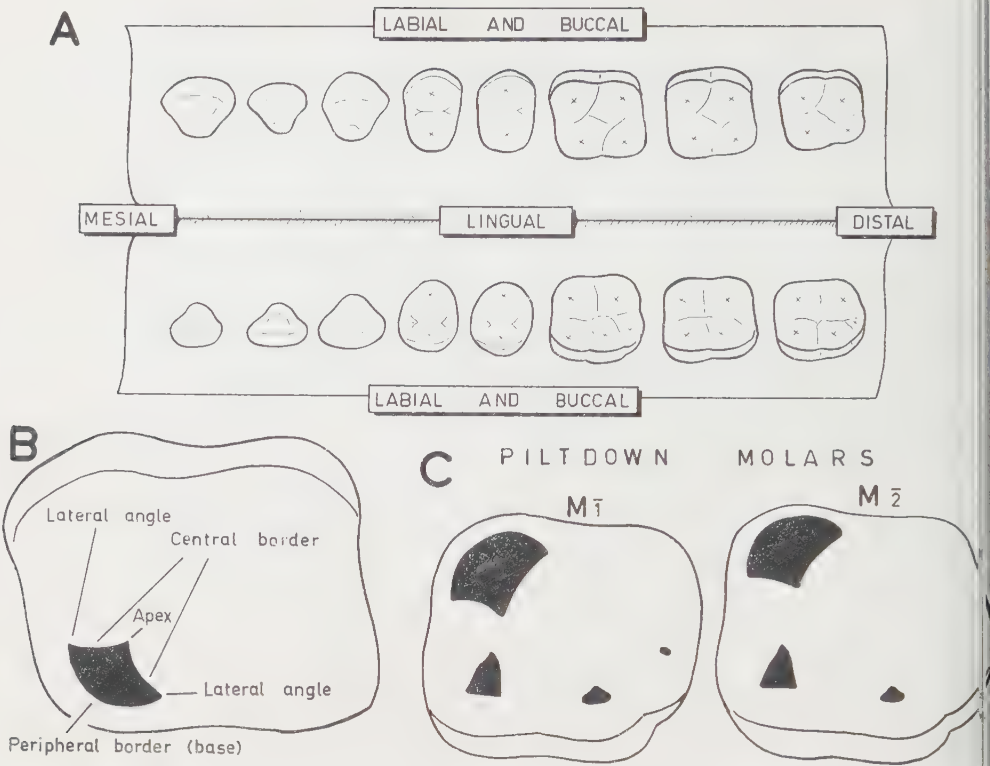

Fig. 1 A, Tooth arch terminology. B, The area of dentine exposure and its terminology C, Patterns of dentine exposure (shaded) in the Piltdown right mandibular first and second molars. Redrawn from illustrations and reversed to facilitate comparison.

sentation at the same degree of tooth attrition. Here one is prefixed with a single lower case letter and the other a double (e.g.: e and ee).

The variants are distinguished by the addition of a numeral to the corresponding lower case letter (e.g.: a3, b1, c2), and are separated from the modal forms by a broken line. The number observed of each form is indicated in the illustrations by a suffix.

From this it is hoped that a broad picture will emerge, not only of the usual sequence of dentine exposure, but also of the range of variation. The study may also be of ethnic interest to the comparative odontologist.

OBSERVATIONS

The dentinal area

In tooth attrition dentine becomes exposed at the center of an attritional facet. It thus comes to form the central of a facet, the remainder of which is surrounding enamel.

The dentinal area, as seen for exam in the cusps of the molar teeth (fig. 1 is characteristically sector-shaped. It be described as having a peripheral bo or base, which is the arc or circumfere of the sector. This border is paralle the enamel edge which separates the clusal from the adjoining side surf The central border is opposite and formed by the two radii of the sector is broken at its mid-point by a projec apex, the center of the sector. The halves of the central border are ge curved. The two borders meet at lat angles.

In the incisor and canine teeth the l ally and lingually disposed borders app to correspond morphologically to per eral and central respectively.

The maxillary teeth

e patterns of exposed dentine (shad-re illustrated in figures 2 and 3. The ence of each form is shown in the rations as a suffix.

ntral incisor. On first exposure of ne (fig. 2, I^1, a) labial and lingual ers meet at sharp lateral angles and ne a narrow area. The lateral angles ne projected laterally and backwards then labial and lingual borders be-separated, changing the lateral an-to lateral sides (c). The lingual border develops a smoothly rounded apex, leaving only an enamel rim (d). The enamel rim becomes lost first lingually (e) and finally completely (f). The variant (b1) is really a transition between the modal forms "a" and "b." It shows that the mesial lateral angle becomes projected laterally and backwards before the distal.

Lateral incisor. The pattern (fig. 2, I^2) follows that of the central incisor in its modal forms. The additional variant (b2) shows that occasionally the distal lateral angle becomes projected laterally and backwards before the mesial.

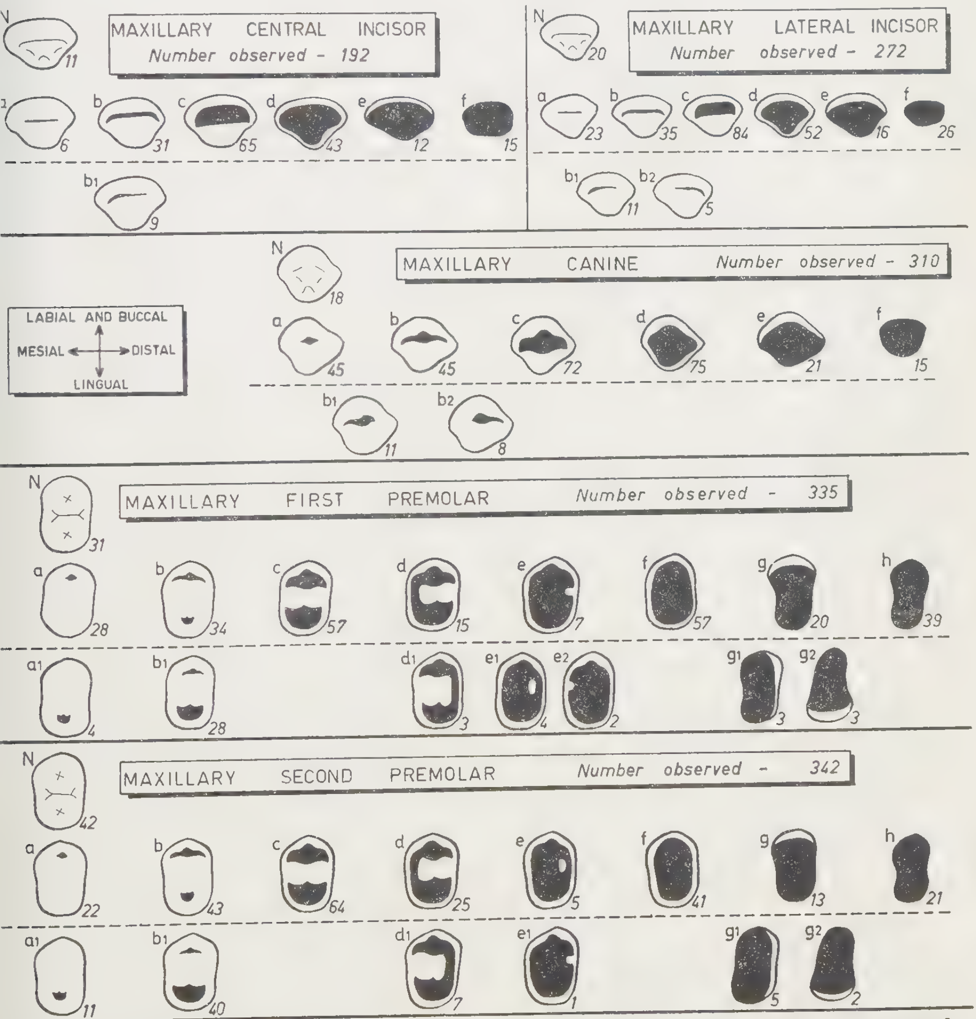

Fig. 2 Patterns of dentine exposure (shaded) in maxillary incisor, canine and premolar teeth. The broken line separates the modal progression (above) from the variants (below). Incidence of each form is shown as a suffix.

Canine. At first the dentinal area is diamond-shaped (fig. 2,^{c}, a). The lateral angles become projected laterally, the labial border develops a well-defined central projection and the lingual border a more smoothly rounded one (b). At this stage the lateral angles are turned slightly backward, giving the whole area an appearance of a bird in flight. Labial and lingual borders become separated, changing the lateral angles to lateral sides (c), and the hypothetical bird in flight appears more massive but with an unaltered wing span. The lingual border develops an apex, leaving only a rim of enamel, and the central projection on the labial border becomes ill-defined (d). Later this central projection becomes completely smoothed with the loss of the enamel rim lingually (e), and finally the enamel rim becomes completely lost (f).

The variants (b1 and b2) show that in the transition from the modal form "a" to "b" the mesial lateral angle is projected laterally before the distal in most cases, but in an appreciable number the reverse obtains.

First premolar. The dentinal area exposed by tooth attrition on the buccal cusp resembles in its first appearance and progressive enlargement that just described for the canine tooth. The area on the lingual cusp is quite different. Here there is a highly-curved peripheral border and a central border which forms approximately a straight line broken by a pointed apex. The lingual area is thus almost a half-circle of small radius.

Dentine is first exposed usually on the buccal cusp (fig. 2, P^1, a) but occasionally on the lingual (a1). The lingual area, however, enlarges more quickly and at the stage where disparity between the two areas can be appreciated the buccal area exceeds the lingual in 34 cases (b), while in 28 the arrangement is the opposite (b1). Later the two areas are equal in size but each retains its distinctive shape (c).

Buccal and lingual areas coalesce usually by a meeting of the mesial lateral angles (d), but occasionally by a meeting of the distal (d1). The peninsula of enamel so formed is reduced from the center until quite small (e) but sometimes an island is cut off by a meeting of distal lateral angles (e1). The va "e2" is a corresponding progressio "d1." Later only a rim of enamel re (f) which becomes lost oftenest ling (g), but sometimes mesially (g1) sometimes buccally (g2). Finally enamel rim is completely lost (h).

Second premolar. The pattern (fi P^2) follows that of the first premolar two minor differences. The inciden peninsula of enamel and cut-off isla enamel becomes transposed (e and and no progression of the variant was observed.

The molar teeth. As previously the dentinal area exposed by tooth tion on the molar cusps is character ally sector-shaped. This shape is ach very soon after the earliest appearan the dentine. As the area enlarges the tor changes from being a little more quarter to being a little less than ha its corresponding circle.

First molar. Dentine is first exp usually on the mesio-lingual cusp (fi M^1, a), and appears in sequence on mesio-buccal (b), disto-buccal (c), disto-lingual cusps (d). Variants on pattern (a1, b1, b2, c1) are few. A four-area stage dentine exposure is us greatest lingually and mesially (d), lingually and distally (d1) and mes and buccally (d2), and occasionally n ly buccally (d3).

The first coalescence usually occu a meeting of the contiguous lateral an of the two lingually-disposed areas. O two free areas the larger is usually mesio-buccal (e), but sometimes the d buccal (e1). Occasionally the contig lateral angles of the two mesially-disp areas meet to form the first coalesce the larger of the two free areas being disto-lingual (e2).

The second coalescence usually oc by the addition of the mesio-buccal to the main mass by its contiguous la angle, leaving the disto-buccal area (f). Sometimes it is the disto-buccal which joins the main mass by its (f1) or by its contiguous lateral a (f2). Apparently as a progression of the disto-buccal area may join the mesi

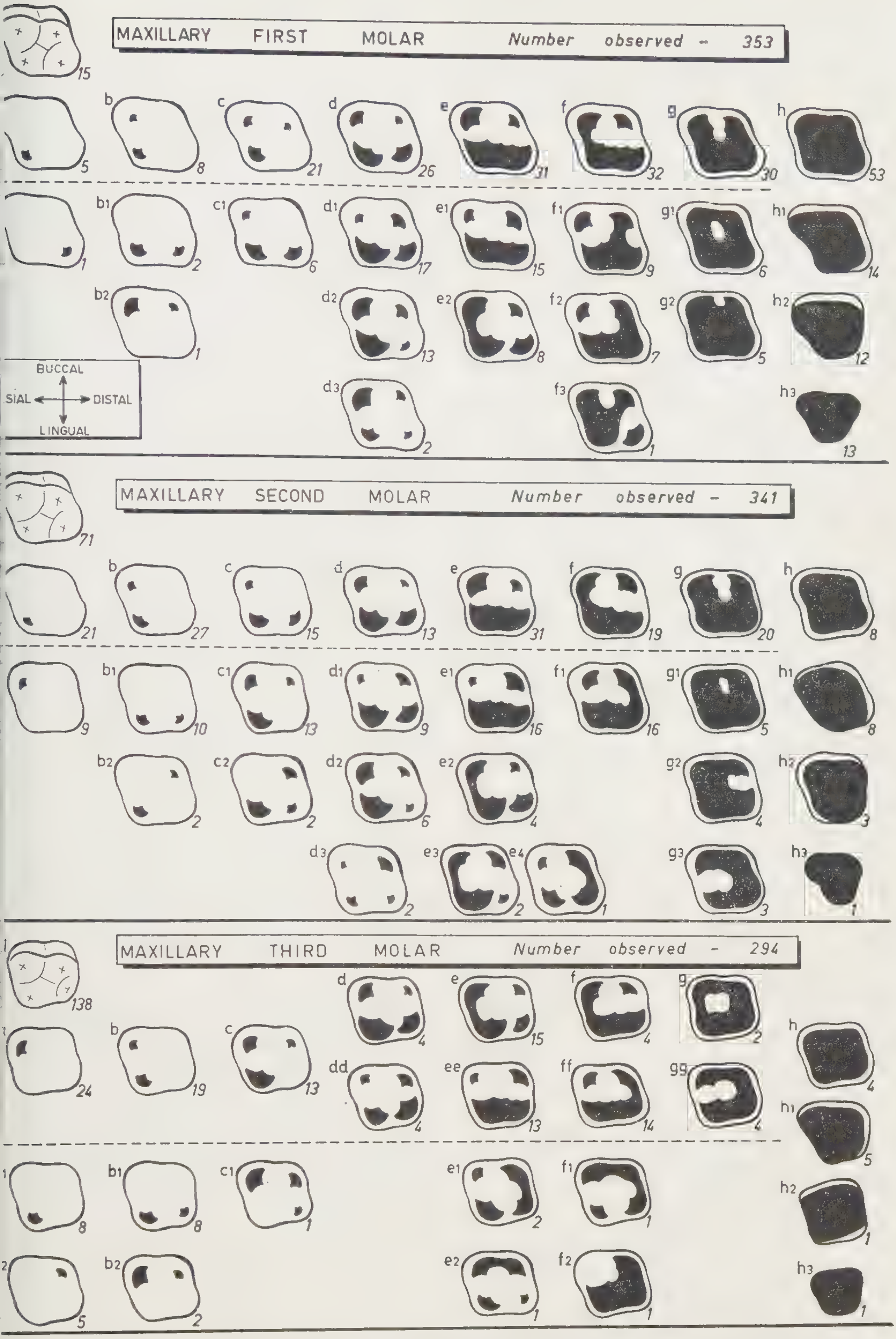

Fig. 3 Patterns of dentine exposure (shaded) in maxillary molar teeth. The broken ne separates the modal progression (above) from the variants (below). Incidence of each rm is shown as a suffix.

disposed main mass by its apex, leaving the disto-lingual area free (f3).

The third coalescence leaves a peninsula of enamel projecting into the now large dentinal area from the buccal aspect of the tooth (g). This peninsula may be cut off to form an island of enamel (g1), or may be progressively reduced from the center (g2).

Lastly a rim of enamel remains (h) which becomes lost mesially (h1), then lingually and distally (h2), and finally completely (h3).

Second molar. Up to the four-area stage the modal progression (fig. 3, M^2) follows that of the first molar. The variants, however, are slightly different and more numerous (a1, b2, c1, c2).

The first coalescence usually also follows the pattern of the first molar (e, e1, e2) but additional variants were noted. In 2 cases involving coalescence of the two mesially-disposed areas the larger of the two free areas is the disto-buccal (e3). In a single variant the first coalescence involves the two distally disposed areas, the larger of the two free areas being in this case the mesio-lingual (e4).

The second coalescence shows less variation than in the first molar. Most often the mesio-buccal area joins the main mass by its contiguous lateral angle, leaving the disto-buccal area free (f). Less often it is the disto-buccal area which joins the main mass by its contiguous lateral angle (f1).

In the third coalescence the peninsula of enamel projecting from the buccal aspect (g) and the cut-off island of enamel (g1) are similar to those described for the first molar. In addition there are cases with peninsulas projecting from the distal aspect (g2) and from the mesial aspect (g3).

Lastly a rim of enamel remains (h) which becomes lost oftenest mesio-lingually (h1), sometimes disto-lingually (h2) and finally completely (h3).

Third molar. A striking difference from the first and second molar teeth is seen in the first exposure of dentine appearing on the mesio-buccal instead of the mesio-lingual cusp (fig. 3, M^3, a). This has few variants (a1 and a2) and fits the modal progression (a-b-c). There can be little

doubt that it is a significant differ
Mesio-lingual (b), disto-buccal (c)
disto-lingual (d) areas are progress
added. At the four-area stage dentin
posure may be greatest lingually and
ally (d) or lingually and distally (

The first coalescence may be bet
the two mesially-disposed areas, wit
disto-lingual being the larger of the
free areas (e); or between the two l
ally-disposed areas, with the disto-b
being the larger free area (ee). In
cases the distally-disposed areas show
ion, with the mesio-lingual the larger
area (e1), and in a single case the
cally-disposed areas, with the mesio-lin
the larger free area (e2).

In the second coalescence the com
est arrangement shows union of the
buccal area with a lingually-disposed
mass, leaving the mesio-buccal area
(ff). A single variant of this form
the free area (f2). The progressio
the commonest earlier form (e), how
is probably a union of the disto-lin
cusp with a mesially-disposed main
leaving the disto-buccal cusp free (f
one case mesio-buccal, disto-buccal
disto-lingual areas show union, lea
the mesio-lingual area free (f1).

The third coalescence may show a p
sula of enamel projecting from the m
aspect of the tooth (gg), or an islan
enamel (g).

Lastly a rim of enamel remains
which may become lost mesially (
mesially and distally (h2), and fi
completely (h3).

The mandibular teeth

The patterns of exposed dentine (
ed) are illustrated in figures 4 and 5.
incidence of each form is shown in
illustrations as a suffix.

Central incisor. The pattern (fig. 4
so closely simulates that of the maxi
central incisor, both in modal progre
and variant, that a separate descri
is unnecessary.

Lateral incisor. Again the pattern
4, I_2) follows that of the correspon
maxillary tooth, even to the addit
variant (b2).

Canine. Here again the pattern o
maxillary canine is closely followed

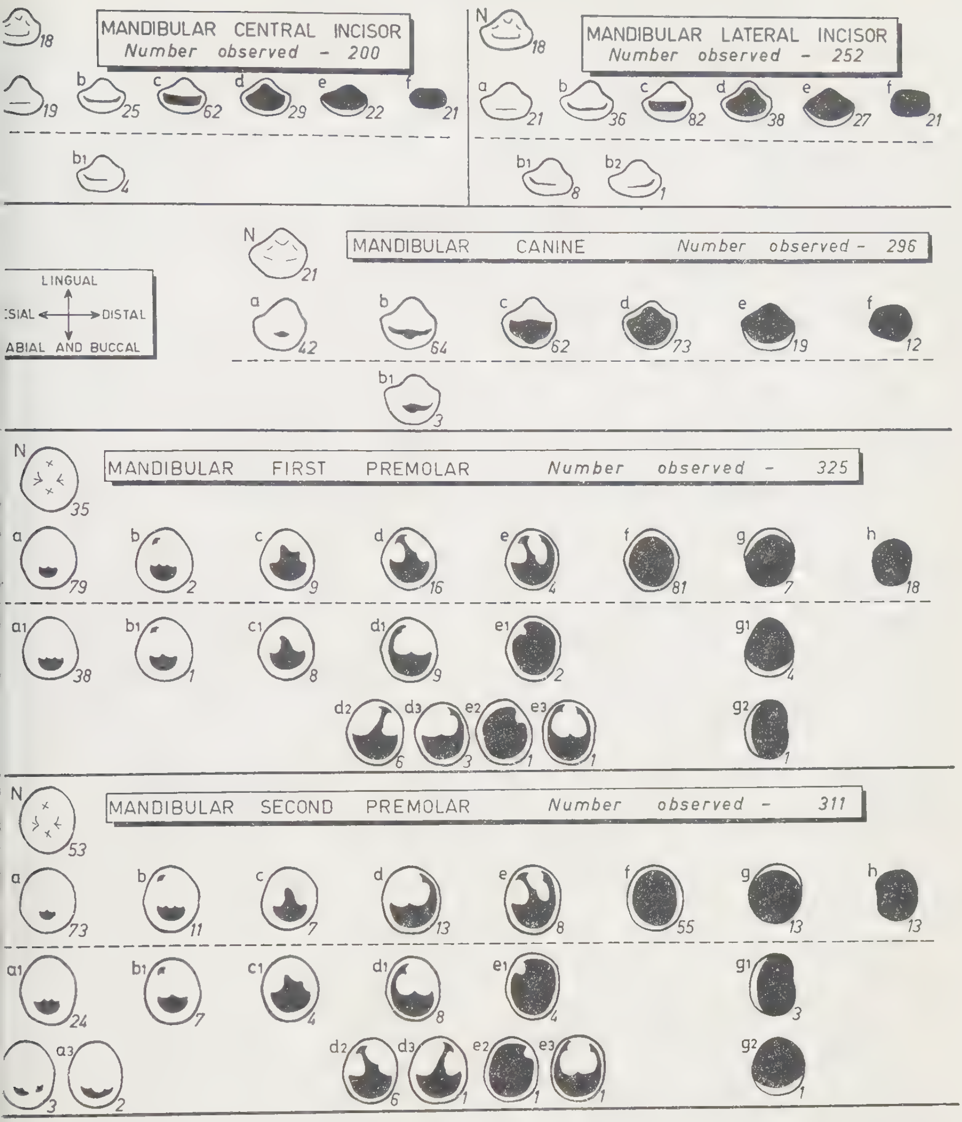

Fig. 4 Patterns of dentine exposure (shaded) in mandibular incisor, canine and premolar :eth. The broken line separates the modal progression (above) from the variants (below). ıcidence of each form is shown as a suffix.

:ansition from form "a" to "b," how- the only variants observed indicate lentinal area first extending in a . direction (fig. 4, c, b1).

:st premolar. The pattern of dentine sure differs materially from that in :orresponding maxillary tooth. The al cusp is very largely involved and ingual to only a minor degree. The : of the dentinal area on the buccal cusp differs both from that of the mandibular canine and that of the maxillary buccal area. On the contrary it resembles in its earlier stages that of the maxillary lingual area. On first exposure of dentine the area has a highly-curved peripheral border and central border which forms approximately a straight line broken by a pointed apex (fig. 4, P_1, a). It forms a half-sector of a circle with relatively

small radius. In many cases the apex is bifid (a1).

The progression from this stage is so variable that it was not possible to demonstrate a satisfactory modal progression as in the other teeth. Sometimes a lingually-placed second dentinal area appears on the mesial side of the transverse axis of the tooth (b and b1). Sometimes the bifid apex extends in a lingual direction (c), and the single apex may behave similarly (c1).

A projection from the apex of the buccal area may coalesce with the apex of the small lingually-disposed area (d). In other cases these join by extension of the mesially-disposed lateral angles (d1). A similar process occasionally involves the buccal area and a small lingually-disposed area which is distal to the transverse axis of the tooth (d2 and d3).

Further extension may involve coalescence of the buccal area with a second small lingually-disposed area. The two lingual areas may extend to the buccal area by the apex of one and the lateral angle of the other (e), or by the two lateral angles (e3). On the other hand the outlined areas of enamel may reduce progressively from the center leaving a small peninsula of enamel from the mesio-lingual aspect (e1) or from the disto-lingual (e2).

Later a rim of enamel remains (f) which becomes lost oftenest buccally (g) but may be lingually (g1) or distally (g2), and finally completely (h).

Second premolar. The pattern (fig. 4, P_2) follows that of the first premolar with a few minor differences. Occasionally two small buccal areas are exposed (a2) and these may coalesce (a3). These appearances may have some connection with bifidity of the apex. Incidence of bifid and single apices at the "c" stage is transposed, as also is the incidence of the variants at the "g" stage. The incidence of the various forms connecting the large buccal to the small lingual areas differs slightly, and probably insignificantly, from that shown for the first premolar.

The molar teeth. In describing the mandibular molar patterns the variable presence of a fifth cusp presents a complication. Its percentage incidence in the

Australian aborigine is stated to be
32.0 and 72.7 in first, second and
molars respectively (Campbell, '25
preliminary review showed that d
exposure on this cusp is in close a
with that on the disto-lingual cus
that these two areas often show ear
sion. Accordingly presence or abse
the fifth cusp was ignored in class
the patterns. This reduces the num
variants. While the four-area sta
cludes a number with a small fifth
this in no way affects the decision
which part of the tooth shows the gr
degree of dentine exposure. Anoth
vantage is that the sequence of
represented by the lower case let
remains comparable with that of the
illary molars.

First molar. Dentine was first ex
in all cases seen on the mesio-bucca
(fig. 5, M_1, a), and the usual sequen
addition was disto-buccal (b), mes
gual (c) and disto-lingual (d). A
stage dentine exposure is usually gr
buccally and distally (d), often bu
and mesially (d1) and rarely mainl
tally (d2). A single variant show
fifth cusp area uniting with the
lingual area instead of the disto-b
(d3).

The first coalescence, ignoring th
the fifth cusp, usually occurs by a me
of the contiguous lateral angles of th
buccally-disposed areas. Of the two
areas the larger is usually the disto-li
(e), but often the mesio-lingual (e1)
casionally the contiguous lateral ang
the two distally-disposed areas me
form the first coalescence, the larg
the two free areas being the mesio-b
(e2).

The second coalescence usually o
by the addition of the mesio-lingual
to the main mass by its contiguous la
angle, leaving the disto-lingual area
(f). In a single variant the fifth
area is also free at this stage (f2).
it is the disto-lingual area which join
main mass by its lateral angle leavin
mesio-lingual area free (f1).

The third coalescence leaves a p
sula of enamel projecting into the
large dentinal area from the lingua
pect of the tooth (g). This peninsula

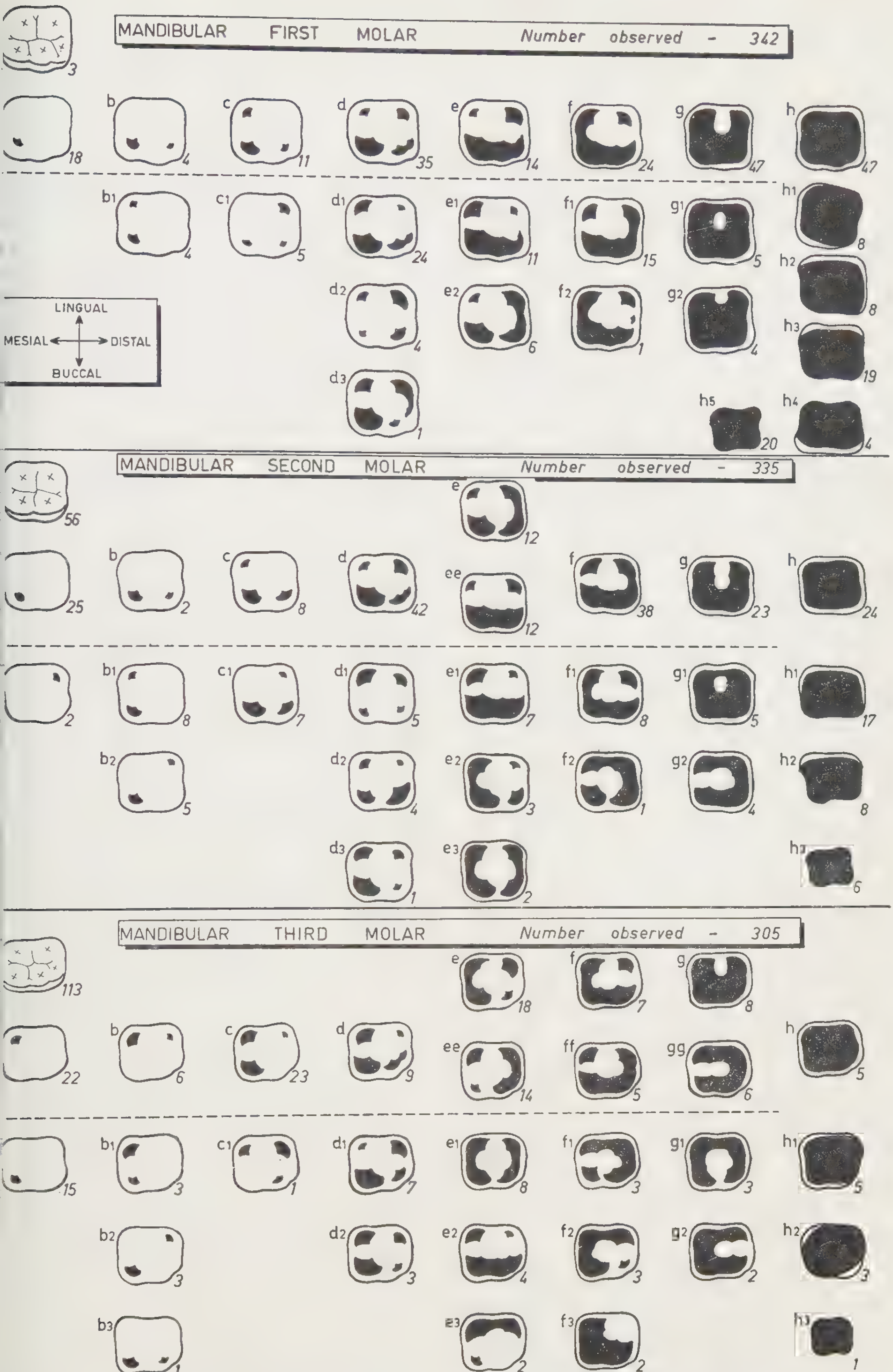

Fig. 5 Patterns of dentine exposure (shaded) in mandibular molar teeth. The broken line separates the modal progression (above) from the variants (below). Incidence of each form is shown as a suffix.

be cut off to form an island of enamel (g1), or may be progressively reduced from the center (g2).

Lastly a rim of enamel remains (h) which becomes lost disto-buccally (h1) or mesio-buccally (h2), then all but lingually (h3), and finally completely (h5). In a few cases the enamel rim is lost all but buccally (h4).

Second molar. Up to the four-area stage the modal progression (fig. 5, M_2) follows that of the first molar. The variants have two additions (a1, b2) and are more numerous.

The first coalescence may follow the pattern of the first molar (ee, e1). Often it is the two distally-disposed areas which show the first coalescence, the larger of the two free areas being the mesio-buccal (e). Occasionally the two mesially-disposed areas coalesce, the larger free area being the disto-buccal (e2). Two cases show separate coalescence of mesially-disposed and distally-disposed areas (e3).

In the second coalescence the incidence of the modal form and first variant seen in the first molar becomes transposed (f, f1). In a single variant the two lingual areas and the disto-buccal show coalescence leaving the mesio-buccal area free (f2).

In the third coalescence the peninsula of enamel projecting from the lingual aspect (g) and the cut-off island of enamel (g1) are similar to those described for the first molar. No instance of the peninsula being reduced from the center was observed. Occasionally a peninsula projects from the mesial aspect of the tooth (g2).

Lastly a rim of enamel remains (h) which becomes lost buccally (h1), then mesially and distally (h2), and finally completely (h3).

Third molar. Dentine is first exposed on the mesio-lingual cusp (fig. 5, M_3, a) in 22 cases against 15 for the mesio-buccal (a1). The difference noted between third molar and first and second in the maxilla is thus paralleled in the mandible, but is less striking. In the modal progression disto-lingual (b), mesio-buccal (c) and disto-buccal (d) areas are progressively added. At the four-area stage dentine exposure may be greatest buccally and mesially (d), buccally and distally (d rarely mesially and lingually (d2).

The first coalescence shows grea ation. Union of the two mesially-d areas is commonest, with the disto- the larger of the two free areas (e). the two distally-disposed areas a volved, with the mesio-lingual the free area (ee). Several cases show ate union of mesially-disposed an tally-disposed areas (e1). Sometim buccally-disposed areas unite leavi mesio-lingual the larger free area Rarely the lingually-disposed areas the two instances seen showing an tional dentinal area only on the buccal cusp (e3).

In the second coalescence the forms resemble those seen to be co est in the first molar (f, ff). Two resemble the commonest form bu no free area of dentine (f3). In instances the two lingual areas an disto-buccal show union, leaving the buccal area free (f1). In another the two lingual areas show union the mesio-buccal area, leaving the buccal free (f2).

The third coalescence shows peni of enamel projecting from the lingu mesial (gg), buccal (g1) and dista aspects of the tooth.

Lastly a rim of enamel remain which becomes lost distally (h1), m and distally (h2), and finally com (h3).

DISCUSSION

The helicoidal occlusal plane

The plane formed by the contiguo clusal surfaces of the teeth in adv attrition has interested several w In the first molar region the plane lateral slope which faces buccally w in the third molar region the latera faces lingually.

This condition has been describ Australian aboriginal (Campbell, African bushman (Drennan, '29), pean neolithic (Cameron, '34, p. Egyptian (Pleasure and Friedman and Eskimo, Maori and Zulu (Moses, '46). Evidently it occurs well-used human dentitions. It ha been described in non-human pr (Campbell, '25; Moses, '46).

rmed "compound attritional" by bell ('25), "twisted" by Drennan and more recently "helicoidal," a borrowed from the physical sciences, kermann ('53), the plane appears to multiple causative factors (Acker- ı, '53; de Boer, '57).

e present study demonstrates a dif- ce in which cusp first shows dentine en the third molar and the two others th jaws. This is doubtless associated the helicoidal occlusal plane and in- s that the causative factors are al- operative at this early stage of tooth ion.

The Piltdown molars

ile this study is primarily intended objective record, it may be profitable -examine the Piltdown teeth in the of the present observations. Only the mandibular first and second molars satisfactorily the pattern of the den- areas in available illustrations. These redrawn reversed to facilitate com- on (fig. 1C).

e dentinal areas. The shape of the wn mesio-buccal areas appears to be le the range of variation presently ibed. Although sector-shaped, each s only about one-eighth of its corres- ing circle. The peripheral border is ht and short, and is not parallel to namel margin. The two halves of the al border form an acute angle at the Both halves are straight with some ular projections.

is contrasts with the dentinal areas e Australian molar cusps. These form rs which range from about one-quar- one-half of the corresponding circle. peripheral border is curved and paral- the enamel margin separating the sal from the adjoining side surface. two halves of the central border are ted by a gentle curve, and the apical ing is never less than a right angle. Gros Clark ('55) points out the un- al flatness of the areas on the mesio- al cusps and their large size relative e areas on the mesio-buccal cusps. e present study, being two-dimen- l, can offer no comment of flatness. Considering the general shape of these areas the apices are seen to be a little off center. As they closely simulate otherwise the shape produced by natural wear, this evidence is insufficient in itself to place them outside the range of variation. Occasionally (fig. 5; M_1, d2; M_2, d1) the mesio-lingual area exceeds in size the mesio-buccal but never to the Piltdown degree.

What is even more striking, however, is that the Piltdown molars, in spite of the large mesio-lingual areas, both lack dentine exposure on the disto-lingual cusps. In the present material the disto-lingual area is more closely in harmony with the mesio-lingual than is the mesio-buccal.

SUMMARY

1. A record is presented of the changing pattern of dentine exposure in each permanent tooth with increasing tooth attrition, as observed in an Australian aboriginal skull collection.

2. The modal progresion is illustrated by an array of commonly occurring forms. The range of variation is indicated by the variants.

3. A comparison is made with the Piltdown teeth redrawn from illustrations.

ACKNOWLEDGMENTS

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dients of Dentine Exposure in Human Molar
th Attrition

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the solution of the Piltdown problem os Clark ('55) raises two dental fea- to the status of taxonomic criteria. are, (1) the pattern of dentine ex- with increasing tooth attrition, and he degree of difference in dentine ure between the molar teeth.

earlier study (Murphy, '59) records sual progression and range of varia- f dentine exposure in each perma- tooth as observed in an Australian inal skull collection. The purpose of esent investigation is to record the of difference in dentine exposure en the molar teeth in each jaw, and en corresponding molar teeth of and lower jaws.

MATERIAL AND METHODS

a were abstracted from the material in the earlier study. The degree of e exposure in each molar tooth was ed in terms of the previous illustra- (Murphy, '59, figs. 3 and 5). The may be defined briefly as follows:

– tooth at occlusal level but no den- xposed.

- dentine exposed on one cusp only.

- dentine exposed on two cusps.

- dentine exposed on three cusps.

- dentine exposed on 4 cusps but the al areas still discrete.

- two dentinal areas coalesced, leav- o free areas.

- three dentinal areas coalesced, g one free area.

- four dentinal areas coalesced, leav- free area, but an island or peninsula mel occupying part of the occlusal e.

- enamel rim completely or partially nding the dentinal area.

variable presence of a fifth cusp gnored in classifying the degree of dentine exposure in the mandibular molars.

In comparing any two molars the degree of difference or gradient was defined as zero where both matched. A minus sign was given where the second of the compared teeth showed a lesser degree of attrition, and a plus sign where it showed a greater. The gradient was recorded as 1 where the degree of attrition matched the adjoining stage, 2 where it matched the one after, and so on progressively.

This provides the advantages of a system of measurement, although an unavoidable defect is that the class intervals may not precisely correspond.

RESULTS

Intermolar gradients

The summated data are tabulated in table 1 and histograms based on the percentage incidence are illustrated in figure 1. Zero values are solid black, minus values hatched and plus values dotted.

The mean gradient between two adjoining molars in either jaw is approximately two. This indicates that by and large the more recently erupted of the two will show a lesser degree of dentine exposure by two stages. The range of variation, however, is such that there can be no assurance in any given case that this gradient will in fact be present.

Variation, as indicated by both range and standard deviation, is greater between second and third molars than between first and second in both jaws.

While the mean gradient between first and second molars is -2.2 in the maxilla, it is -1.7 in the mandible. The difference between these means is statistically significant by the "t" test at the level $P < 0.001$. This means that in the mandible

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TABLE 1

Intermolar gradients

(Difference in degree of dentine exposure as defined in the text)

Gradient	Maxillary molars						Mandibular molars				
	$M^1 \rightarrow M^2$		$M^2 \rightarrow M^3$		$M^1 \rightarrow M^3$		$M_1 \rightarrow M_2$		$M_2 \rightarrow M_3$		M
	No.	%	No.	%	No.	%	No.	%	No.	%	No.
−8			1	0.4	14	6.1					9
−7			5	2.2	17	7.4			5	2.2	14
−6	1	0.4	7	3.0	41	17.8	4	1.7	3	1.3	33
−5	11	4.8	20	8.7	40	17.4	0	0.0	15	6.5	34
−4	15	6.5	19	8.3	38	16.5	13	5.6	38	16.4	54
−3	58	25.2	36	15.7	35	15.2	42	18.1	36	15.5	29
−2	78	33.9	42	18.3	22	9.6	64	27.6	50	21.5	24
−1	48	20.9	61	26.5	19	8.3	63	27.2	49	21.1	20
0	16	7.0	26	11.3	3	1.3	42	18.1	20	8.6	10
+1	3	1.3	11	4.8	0	0.0	3	1.3	11	4.7	5
+2			1	0.4	1	0.4	1	0.4	5	2.2	
+3			1	0.4							
Totals	230	100.0	230	100.0	230	100.0	232	100.0	232	100.0	232
Mean	−2.2		−2.2		−4.3		−1.7		−2.2		
Range	−6::+1		−8::+3		−8::+2		−6::+2		−7::+2		−
St. dev.	1.263		1.938		2.016		1.325		1.848		2

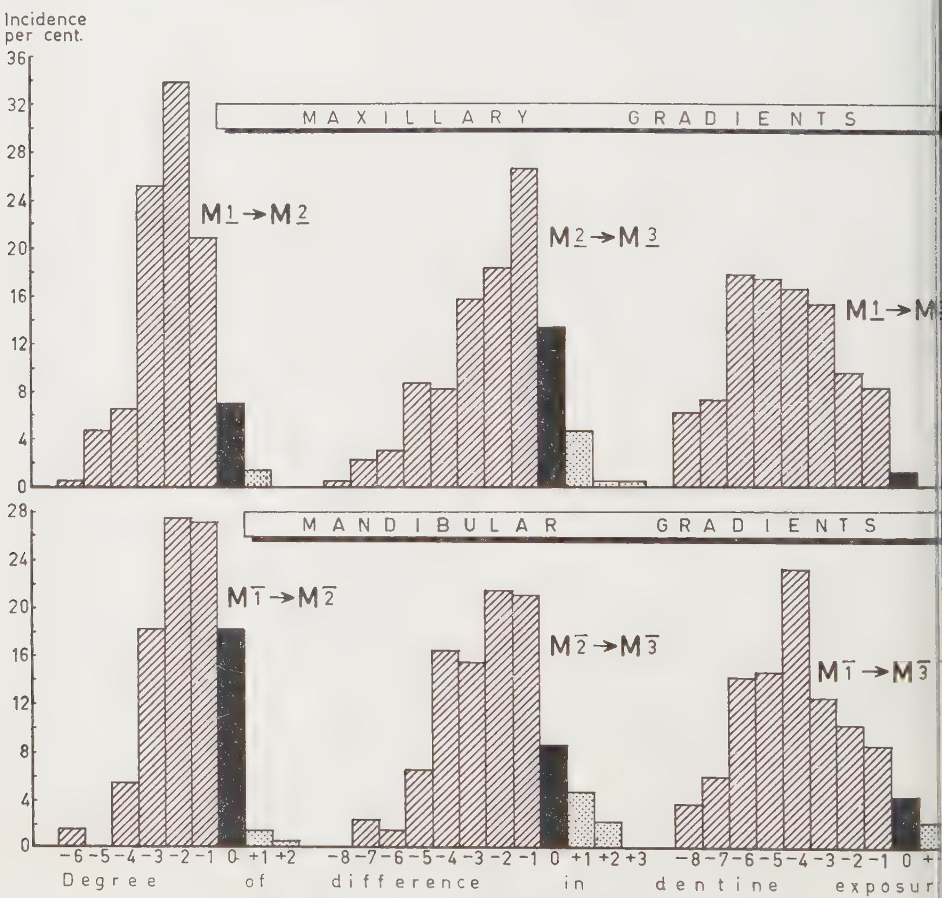

Fig. 1 Intermolar gradients of dentine exposure. Zero values are solid black, mi values hatched and plus values dotted. Data from table 1.

;econd molar more nearly approaches lentine exposure of the first than is :ase in the maxilla. This is reflected he differing incidence of zero and values, where the second molar equals exceeds respectively the degree of ine exposure of the first. These num- 19.8% in the mandible against 8.3% ie maxilla.

ie mean gradient between first and molars is −4.3 in the maxilla and in the mandible. This difference is statistically significant by the "t" but the greater dispersion reduces ;ignificance level to $P < 0.05$.

ie mean gradient between second and molars is −2.2 in both jaws. In all ;sponding pairs the variances do not ficantly differ when the figures are ected to the "z" test.

iese facts indicate that the essential rence between the jaws in dentine ex- re lies in the gradients between the and second molar teeth. It seemed hwhile, therefore, to examine the condition present at the various degrees of dentine exposure.

In studying the analyzed data (table 2 and figure 2) it should be noted that when the first molar is at the "a" stage the gradient cannot exceed −1, at "b" it cannot exceed −2 and at "c" −3. In the rise to the peak of the curve the gradient in the mandible is slightly the greater, while

TABLE 2

Gradient between first and second molar teeth according to degree of dentine exposure in first molar

Degree of M^1	Maxilla		Mandible	
	No.	Mean gradient	No.	Mean gradient
a	3	−0.7	7	−1.0
b	4	−1.5	4	−1.8
c	16	−2.6	12	−2.9
d	32	−2.9	39	−2.4
e	34	−2.5	31	−1.5
f	37	−2.2	37	−1.7
g	35	−2.1	33	−1.7
h	69	−1.9	73	−1.5
Total	230	−2.2	232	−1.7

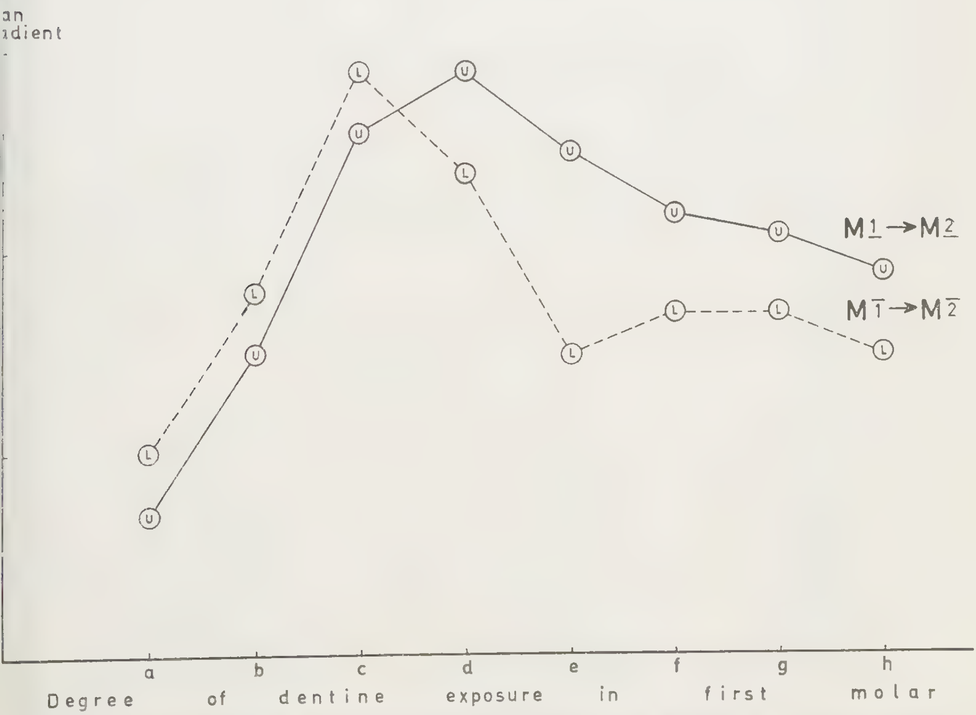

Fig. 2 Mean intermolar gradients analyzed according to degree of dentine exposure. Data from table 2.

in the fall it is considerably the lesser. In early stages of dentine exposure, therefore, the first molar exceeds the second to a slightly greater degree in the mandible than in the maxilla. In later stages of dentine exposure the first molar exceeds the second to a considerably lesser degree in the mandible than in the maxilla.

This indicates also that the signi[illegible] difference in mean gradients noted i[illegible] summated data are due to difference[illegible] curring at later stages of dentine expo[illegible]

Interjaw gradients

The degree of dentine exposure i[illegible] responding molar teeth of upper and l[illegible]

TABLE 3
Interjaw gradients
(Difference in degree of dentine exposure as defined in the text)

Gradient	First molars $M^1 \rightarrow M_1$		Second molars $M^2 \rightarrow M_2$		Third molars $M^3 \rightarrow M_3$	
	No.	%	No.	%	No.	%
−6					1	0.6
−5					0	0.0
−4					2	1.1
−3			1	0.4	1	0.6
−2	7	2.6	7	2.7	4	2.3
−1	35	13.1	28	10.7	22	12.7
0	112	41.8	53	20.3	30	17.4
+1	76	28.3	80	30.6	41	23.7
+2	31	11.6	59	22.6	35	20.2
+3	6	2.2	24	9.2	24	13.9
+4	1	0.4	8	3.1	6	3.5
+5			1	0.4	4	2.3
+6					2	1.1
+7					1	0.6
Totals	268	100.0	261	100.0	173	100.0
Mean	+ 0.4		+ 1.0		+ 1.1	
Range	−2::+4		−3::+5		−6::+7	
St. dev.	1.035		1.366		1.875	

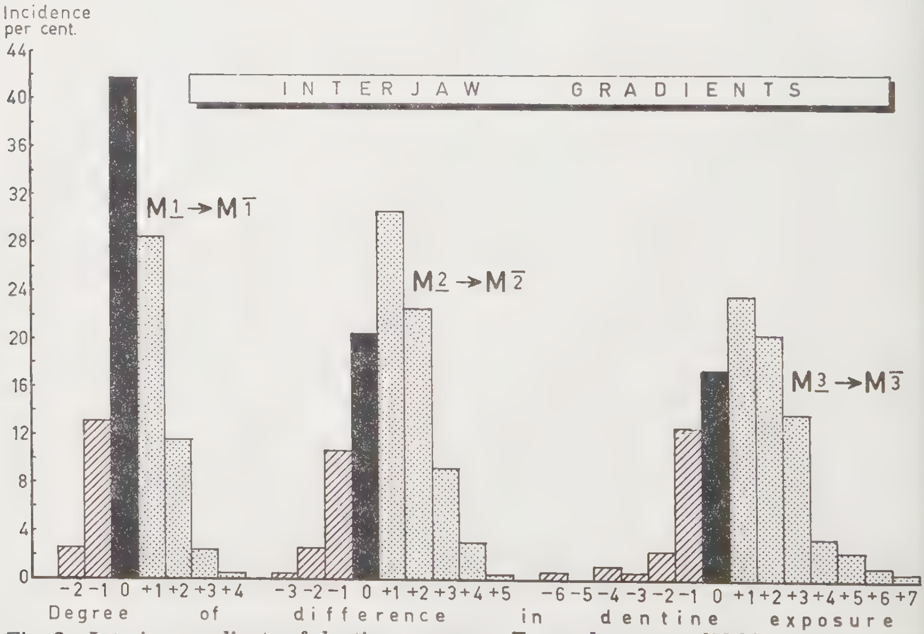

Fig. 3 Interjaw gradients of dentine exposure. Zero values are solid black, minus values hatched and plus values dotted. Data from table 3.

was compared in the manner de-
ed for the molars of the same jaw.
ıe results are tabulated in table 3
histograms based on the percentage
.ence are illustrated in figure 3. Again
values are solid black, minus values
ıed and plus values dotted.

In all three comparisons the mandibular molar shows a more advanced degree of dentine exposure than the maxillary. The gradient in the first molars is small (mean +0.4) but is significantly different from zero at the level $P < 0.001$ by the "t" test. The gradient is appreciably greater in the

TABLE 4

Gradient between corresponding maxillary and mandibular molar teeth according to degree of dentine exposure in maxillary molar

Degree of M^1	No.	Mean gradient	Degree of M^2	No.	Mean gradient	Degree of M^3	No.	Mean gradient
N	10	+1.0	N	21	+1.5	N	35	+2.1
a	5	+0.8	a	28	+0.9	a	34	+1.6
b	10	+0.6	b	37	+1.6	b	27	+1.3
c	27	+0.2	c	29	+1.6	c	14	+1.5
d	54	+0.4	d	27	+0.7	d	8	+0.4
e	52	+0.8	e	48	+1.3	e	29	+0.6
f	44	+0.6	f	31	+0.7	f	16	+0.3
g	36	+0.3	g	28	−0.1	g	5	−1.2
h	30	−0.4	h	12	−0.3	h	5	−1.6
Total	268	+0.4		261	+1.0		173	+1.1

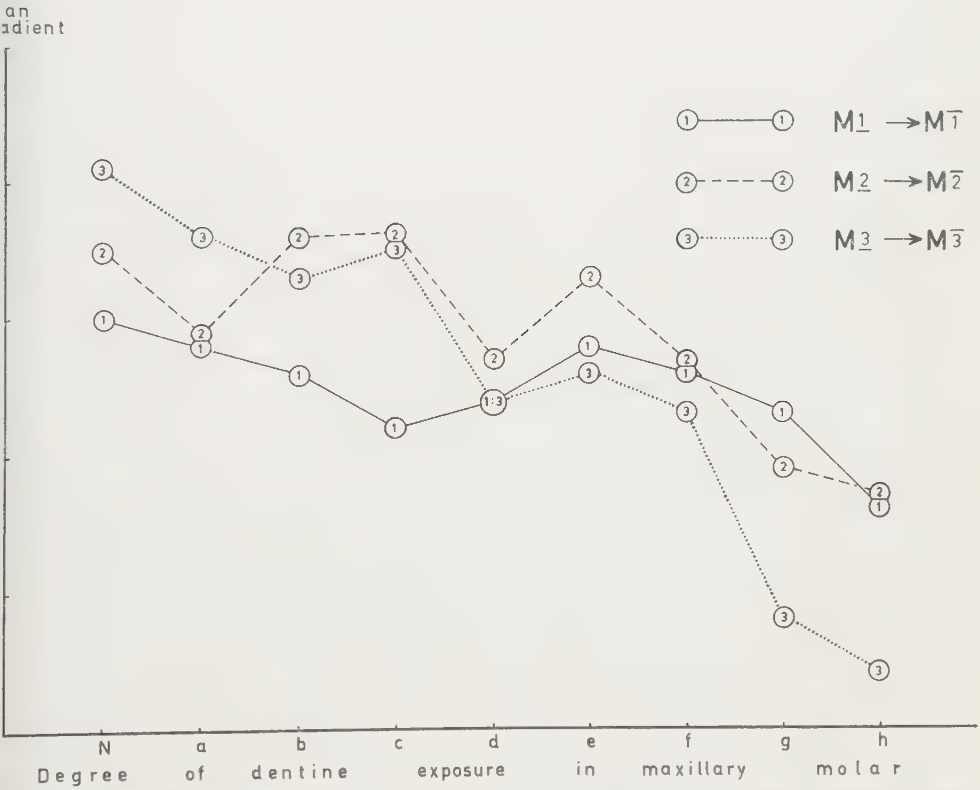

Fig. 4 Mean interjaw gradients analyzed according to degree of dentine exposure. Data from table 4.

second (mean +1.0) and in the third (mean +1.1). The slight difference between these two is statistically insignificant. The difference between the first molar mean and each of the others is significant at the level $P < 0.001$ by the "t" test.

The data, analyzed according to the degree of dentine exposure (table 4 and figure 4), show that the greatest difference between the mandibular molar and its maxillary counterpart is in the early stages of attrition. When the maxillary first molar is at occlusal level with the enamel covering still complete, the mandibular shows dentine already exposed on one cusp in the average case. The corresponding condition with the third molars shows dentine on two mandibular cusps, while the second molars occupy an intermediate position.

It should be noted that when the maxillary molar is at the "h" stage the gradient cannot be a plus value. Allowing for this defect inherent in the method there is clearly a trend towards equalization of the amount of dentine exposed with increasing tooth attrition.

That the dispersion increases along the molar series is indicated by the increasing range and standard deviation. Variance differences between first and second molar gradients and between second and third are both statistically significant at the level $P < 0.001$ by the "z" test.

DISCUSSION

The intermolar gradient

In Marston's ('52) contribution to the Piltdown problem he concludes, from the approximately equal degree of wear in the Piltdown molars, that the second erupted, ". . . as in the apes, fairly soon after the first, and without the more prolonged time interval of man." Le Gros Clark ('55) states, however, that such cases do occur exceptionally in man and suggests that this may happen " . . . as the result of some defect in the upper dentition."

As the Piltdown molars both match the lower case letter "c" of the present study, the gradient between them is zero. This gradient, or one in which the second molar shows more advanced dentine exposure than the first, is seen in no less than 19.8% in the mandibles of the present mat (table 1, fig. 1). The corresponding ure in the maxilla is 8.3%. These fig moreover, were obtained from denti which are characterized by a lack o fects. This supports Koski and Garn's (contention that the use of the degree o trition as an indirect indication of eru sequence is "a very dangerous one."

The analyzed data (table 2, fig. however, show that at stage "c" a gradient is usually present. Referenc the raw data fails to disclose any gradients at this stage. Of the 16 m dibles containing first molars at the stage 13 still retained the second m also. Of these one had not reached occlusal level, 11 had reached this but lacked dentine exposure, and showed dentine on a single cusp, the stage. Examined from the opposite rection, of the 15 mandibles contai second molars at the "c" stage, 13 retained the first molar also. Of the had reached the "d" stage, 2 the "e," 6 the "f."

These facts suggest that Le Gros Cla ('55) use of the method with the Piltd molars is still a valid one.

The interjaw gradient

The fallibility of using the degree o trition as an indirect indication of e tion sequence is further emphasized by interjaw gradients of dentine expo found in the present study (table 3, fig. An a priori assumption that corresp ing molars of upper and lower jaws w show the same degree of dentine expo seems a perfectly reasonable one. Yet first mandibular molar exceeds the ma lary by a margin which is greater t zero at a high level of significance. In respect the second and third pairs of lars agree with each other, but the grad in both differs, also at a high level of nificance, not only from zero, but from the gradient obtaining in the molars.

The variances differ significantly al the cheek teeth series. This is an exp sion of increasing variability, also o ous in the histograms, and is in acc with Butler's ('39) "field concept" of mo ization.

Functional implications

sky and Fisher ('53, p. 223) state ooth attrition is " . . . the resultant ong masticatory function." This the question: Can this study of e exposure throw light on the con- sial subject of masticatory function? iation of dentine exposure may be ed from additional factors. These fferences in type of food, in timing equence of tooth eruption, in tooth and in positioning of individual teeth e to the arch as a whole. Also in- l may be differences in the thickness e enamel covering and possibly dif- es in enamel hardness. Again the al area is only part of the attritional which includes the surrounding el whose extent of wear is outside ope of this study.

eems likely, however, that in a large factors other than masticatory func- would cancel each other out. Thus resent findings carry the following ations on masticatory function:

In the dynamics of human mastica- ttritioning stresses are not uniform therto supposed or tacitly assumed Ackermann, '53, p. 124).

An equal degree of attritioning stress red by the second and third molars ch jaw. With increasing tooth attri- this degree becomes progressively er than that borne by the first molar. the degree of attrition in the molar of each jaw tends to equalize. This is significantly greater in the man- than in the maxilla.

In corresponding molar teeth of up- nd lower jaws the lower is initially cted to a greater degree of attritioning . This occurs to an equal extent in econd and third molar teeth. It oc- to a significantly lesser extent in the molars. With increasing tooth attri- this differential attritioning stress be- n the jaws becomes progressively less. the degree of attrition in correspond- pper and lower molars tends to equal-

Taxonomic considerations

arston's ('52) method of distinguish- uman from anthropoid tooth wear is based on differences in the architecture of the temporomandibular joints and in the transgressions of the lower teeth across the upper in chewing. These premises are themselves highly controversial. The more recent comparative work of Ashton and Zuckerman ('54) and Mills ('55) respectively suggests that the differences are of degree only and are less fundamental than formerly supposed.

A more direct method is to investigate anthropoid dentine exposure in a collection extensive enough to match the present studies. From the two there might emerge a tool useful in primate taxonomy.

SUMMARY

1. Degrees of dentine exposure were recorded from the molar teeth of an Australian aboriginal skull collection.

2. A comparison is made of the degree of difference in dentine exposure between the molar teeth in each jaw—the intermolar gradient.

3. A comparison is made of the degree of difference in dentine exposure between corresponding molars of upper and lower jaws—the interjaw gradient.

4. The observations and their implications are discussed.

ACKNOWLEDGMENTS

Again I must thank Professor A. A. Abbie for advice and criticism, and the Director and Ethnologist of the South Australian Museum for continuing courtesies. Miss Judith Schroder of this department gave statistical help.

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od Groups of Alaskan Eskimos and Indians

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The Blood Grouping Laboratory of Boston,[1] National Institute for Medical Research, London, and National Institute of Arthritis and Metabolic Diseases, National Institutes of Health, Bethesda, Md.

ıring the course of recent field work aska, blood specimens were collected Eskimos and Indians for blood group- ınd other investigations. This paper ds the results of blood group tests provides a basis for comparison with ıgs in other groups of indigenous ricans. Other investigations of gene- y determined metabolic traits carried n the same populations included he- obin and haptoglobin analyses (Blum- et al., '59), red-cell enzymes (Keller- r et al., '59), urinary amino acid ex- ɔn patterns (Allison et al., '59), and -testing with phenylthiocarbamide son and Blumberg, '59). A full dis- on of the anthropological significance ese findings will be presented later.

Populations from which samples were taken

The Eskimos were all northern dialect (Inupik) speakers (fig. 1). The first group consisted of 111 people out of 220 living in Wainwright; the second of 64 not-closely-related inhabitants of the large town of Barrow; the third of 55 people out of a total of approximately 70 now living near Summit Lake in Anaktuvuk Pass in the Brooks Range. Of the 70, approximately 10 were three years or younger from whom no attempt was made to remove blood. The fourth group consisted of 11 full-blooded Eskimos derived from the

[1] Supported in part by grant G-3524 from the National Institutes of Health.

ʼig. 1 Outline map of Alaska showing the locations at which blood collections were made.

Arctic slope now living in the mixed Eskimo-Indian community of Beaver on the Yukon River.

The northern Athabascan speaking Indians included 78 out of a total of approximately 110 from Arctic Village, Brooks Range, 110 from Fort Yukon and 18 from Beaver. The majority of the Aborigines tested were recorded as full blooded in the census records, and were regarded as being so in their communities. However, in Wainwright and Fort Yukon approximately 15% were listed as more than half, but less than full blooded. Tlingits were obtained from Mt. Edgecombe and Sitka, all but 5 of them being recorded as full blooded and the remainder as 3/4 or 7/8 Indian.

In some of the communities (those of Wainwright, Anaktuvuk Pass, Arctic Village and Beaver) a large proportion of the population was sampled, and the results include several members of the same sibship. Exogamy is common, and only one instance of a first-cousin marriage appeared in kinships from Wainwright, Anaktuvuk, Arctic Village, and Beaver. The findings in these various villages are sufficiently different one from another that it was considered advisable to list them separately (tables 1–4).

METHODS OF STUDY

Blood specimens were collected by v puncture using Vacutainers without coagulant (Becton, Dickinson and C pany, Rutherford, N. J.). Specimens kept at 4°C and dispatched to the B Grouping Laboratory, Boston, withir hours of collection. Travelling time Alaska to Boston was approximately hours for each lot except for the firs samples from the Tlingits which were layed in transit. All samples except t of 49 of the Tlingits arrived in Bosto excellent condition. Those 49 Tl bloods were in relatively poor condi and gave unsatisfactory results with t and Lewis serums.

Reagents and the methods of their are outlined in table 5. Anti-A_1 was only on A and AB bloods. Anti-D plu and anti-G were used only on the D-n tive. Anti-rh_i was used only with C- tives, anti-k with K-positives. Tests w deemed satisfactory with the exceptio the tests for P and Lewis in the firs Tlingits. The tests for P and Lewis on Beavers were omitted because of lac time. Anti-Vel was tested only with since the serum was from a type O do

TABLE 1

Phenotype and gene frequencies—A-B-O groups of Alaskans

	Alaskan Eskimos				Alaskan Indians			
	Wainwright	Barrow	Anaktuvuk Pass	Beaver	Arctic Village	Fort Yukon	Beaver	Tlin
Phenotypes								
O	33	17	9	6	74	92	15	63
	.30	.27	.16	.55	.95	.84	.83	.
A_1	58	42	29	5	4	16	3	11
	.52	.66	.53	.45	.05	.14	.17	.
A_2	1	1	0	0	0	2	0	0
	.01	.02				.02		
B	13	4	12	0	0	0	0	4
	.12	.06	.22					.
A_1B	6	0	5	0	0	0	0	1
	.05		.09					.
Total	111	64	55	11	78	110	18	79
Genes								
O	.55	.54	.44	—	.97	.915	—	.
A_1	.35	.41	.39	—	.03	.075	—	.
A_2	.005	.02	.00	—	.00	.01	—	.
B	.09	.03	.17	—	.00	.00	—	.

TABLE 2

Phenotype and gene frequencies—Rh groups of Alaskans

	Alaskan Eskimos				Alaskan Indians			
	Wainwright	Barrow	Anaktuvuk Pass	Beaver	Arctic Village	Fort Yukon	Beaver	Tlingit
pes								
	1 *.01*	3 *.05*	0	1 *.09*	7 *.09*	11 *.10*	0	6 *.08*
	24 *.22*	19 *.30*	15 *.27*	4 *.36*	23 *.295*	44 *.40*	6 *.33*	37 *.47*
	65 *.59*	28 *.44*	30 *.55*	4 *.36*	34 *.44*	38 *.345*	10 *.56*	23 *.29*
	20 *.18*	11 *.17*	10 *.18*	2 *.18*	7 *.09*	9 *.08*	1 *.06*	7 *.09*
	1 *.01*	3 *.05*	0	0	1 *.01*	6 *.055*	0	3 *.04*
	0	0	0	0	3 *.04*	0	1 *.06*	2 *.03*
	0	0	0	0	2 *.03*	1 *.01*	0	0
	0	0	0	0	1 *.01*	0	0	0
	0	0	0	0	0	0	0	1 *.01*
rh	0	0	0	0	0	1 *.01*	0	0
	111	64	55	11	78	110	18	79
	.51	*.54*	*.55*	—	*.58*	*.62*	—	*.60*
	.48	*.41*	*.45*	—	*.33*	*.29*[1]	—	*.25*
	.01	*.05*	*.00*	—	*.06*	*.08*	—	*.063*
	.00	*.00*	*.00*	—	*.03*	*.0045*	—	*.013*
	.00	*.00*	*.00*	—	*.00*	*.00*	—	*.066*

udes the one known D^u variant.

TABLE 3

Phenotype and gene frequencies—M-N-S groups of Alaskans

	Alaskan Eskimos				Alaskan Indians			
	Wainwright	Barrow	Anaktuvuk Pass	Beaver	Arctic Village	Fort Yukon	Beaver	Tlingit
pes								
	49 *.44*	25 *.39*	42 *.76*	5 *.45*	56 *.72*	47 *.43*	6 *.33*	42 *.53*
	24 *.22*	14 *.22*	1 *.02*	1 *.09*	16 *.205*	23 *.21*	10 *.56*	15 *.19*
	29 *.26*	19 *.30*	10 *.18*	3 *.27*	5 *.06*	18 *.16*	0	15 *.19*
	8 *.07*	5 *.08*	2 *.04*	1 *.09*	1 *.01*	22 *.20*	1 *.06*	7 *.09*
	1 *.01*	1 *.02*	0	0	0	0	0	0
	0	0	0	1 *.09*	0	0	1 *.06*	0
	111	64	55	11	78	110	18	79
	.82	*.80*	*.89*	—	*.96*	*.82*	—	*.86*
	.18	*.20*	*.11*	—	*.038*	*.18*	—	*.14*
	.16	*.16*	*.03*	—	*.12*	*.23*	—	*.15*
	.66	*.63*	*.87*	—	*.85*	*.65*	—	*.73*
	.16	*.17*	*.02*	—	*.115*	*.16*	—	*.13*
	.18	*.20*	*.10*	—	*.037*	*.115*	—	*.12*
	.00	*.00*	*.01*	Present	*.001*	*.067*	Present	*.02*

Calculations of gene frequencies

O was obtained from the square root of the frequency of type O. Similarly, the frequencies for *Ms* were obtained by taking the square root of the frequency of phenotype M,S−. Frequencies for all the Rh genes, and for *M*, *N*, and the genes of the Kell system were obtained by direct count. For this purpose individuals of phenotype Rh_2Rh_2, for example, were considered to be of genotype R^2R^2, etc. Since no R^0, r', or r^y genes were identifie[d], impossible to guess how many (if a[ny]) the supposed r, R^1, and R^z genes were [really] R^0, r', or r^y. It is certain that none o[f these] genes are common in this populati[on].

Frequencies for A, A_1, B, S, Fy^a, [...] and Di^a were obtained from the for[mula]

$$\text{Frequency X} = 1 - \sqrt{\text{frequency of X-nega[tive]}}$$

The frequency of *MS* was obtained b[y sub]tracting *Ms* from *M*. The frequency [...]

TABLE 4

Phenotype and gene frequencies—other blood groups in Alaskans

	Alaskan Eskimos				Alaskan Indians		
	Wainwright	Barrow	Anaktuvuk Pass	Beaver	Arctic Village	Fort Yukon	Beaver
Phenotypes							
Fy(a+)	106 .955	64 1.00	55 1.00	11 1.00	77 .99	110 1.00	18 1.00
Fy(a−)	5 .045	0	0	0	1 .013	0	0
Jk(a+)	78 .70	43 .67	39 .71	10 .91	60 .77	79 .72	14 .78
Jk(a−)	33 .30	21 .33	16 .29	1 .09	18 .23	31 .28	4 .22
P+	19 .17	24 .38	20 .36	*	14 .18	33 .33	*
P−	92 .83	40 .62	35 .64	*	63 .82	66 .67	*
Le(a+b−)	0	0	0	*	0	0	*
Le(a−b+)	109 .98	61 .95	55 1.00	*	73 .95	94 .95	*
Le(a−b−)	2 .02	3 .05	0	*	4 .052	5 .05	*
K+Kp(a−)	0	0	0	0	0	1 .009	0
K−Kp(a+)	1 .01	0	0	0	0	0	0
K−Kp(a−)	110 .99	64 1.00	55 1.00	11 1.00	78 1.00	109 .99	18 1.00
Di(a+)	2 .02	0	0	0	0	1 .009	0
Di(a−)	109 .98	64 1.00	55 1.00	11 1.00	78 1.00	109 .99	18 1.00
Genes							
Fy^a	.79	1.00	1.00	—	.89	1.00	—
Jk^a	.46	.43	.46	—	.52	.47	—
P	.09	.21	.20	—	.10	.18	—
K^b	.00	.00	.00	—	.00	.004	—
k^a	.004	.00	.00	—	.00	.00	—
k^b	.996	1.00	1.00	—	1.00	.996	—
Di^a	.01	.00	.00	—	.00	.004	—

* Not done

TABLE 5
Reagents used in testing Alaskans

	Lot no.	Source	Method of use
	SA 127	BGL	Saline tube test
	SB 116	BGL	Saline tube test
	SAA 56	BGL	Saline tube test
	Ulex 38	BGL	Saline tube test
	SRC 77	BGL	Saline tube test
	ARCW 67	BGL	Albumin tube test
	ARD 38	BGL	Albumin tube test
	ARE 117	BGL	Albumin tube test
	—	T. J. Greenwalt	Indirect Coombs test
	AHC 67	BGL	Albumin tube test
	AHE 67	BGL	Albumin tube test
- D^u	CRDU 68	BGL	Indirect Coombs test
	ARDC 68	BGL	Albumin tube test
	Cla.	R. E. Rosenfield	Ficin technique
l	Bau	R. E. Rosenfield	Ficin technique
	SM 117	BGL	Saline tube test
	N15	Ortho	Saline tube test
	SFA 237	R. E. Rosenfield	Saline tube test
	SMG 97	BGL	Saline tube test
	SVW 58	BGL	Saline tube test
	UB 4	J. F. Mohn	Saline tube test
	CK 117	BGL	Indirect Coombs test
	M.N.	P. J. Schmidt	Indirect Coombs test
a	CKPA 97B	BGL	Indirect Coombs test
b	CKPB 116	BGL	Indirect Coombs test
	CFYA 97B	BGL	Indirect Coombs test
	CJKA 48	BGL	Indirect Coombs test
	Mc C.	BGL	Indirect Coombs test
	Daw.	BGL	Saline (cold)
	SP 27	BGL	Saline (cold)
	SLEA 47	BGL	Saline (cold)
	Mc G. 56	BGL	Saline (cold)
a	Gin.	BGL	Saline tube test
	Woj.	J. F. Mohn	Indirect Coombs test
	—	M. Layrisse	Indirect Coombs test
-a	SWRA 18B	BGL	Saline tube test
a	—	K. Stern	Indirect Coombs test
l	—	J. J. van Loghem	Saline tube test
	—	R. E. Rosenfield	Indirect Coombs test

Rosenfield, R. E., '58. [2] See Giblett, E. R., '58.

btained by subtracting MS from S. rly, $Ns = N - NS$. Expected pheno- requencies, calculated from the gene ncies as shown in the tables, fitted the observed frequencies. Gene ncies for A, B, and O were corrected necessary, using Bernstein's simple tion. In the Tlingit group, the fre- y of r'' was derived from the formula

$\sqrt{r^2 \text{ plus observed frequency type rh}''} - r$,

resulted in a calculated frequency of 0.066, indicating that about 9 of 05 supposed R^2 genes in this popula- nay actually be r''. The frequency of counted was therefore reduced cor- ndingly.

RESULTS

Most of the data are contained in tables 1–4. In addition 239 Eskimos and 255 Indians were tested with anti-Mg, all with negative results. 241 Eskimos and 255 Indians were all negative with anti-Lu^a. 241 Eskimos and 223 Indians were all positive with anti-Kp^b. 241 Eskimos and 255 Indians were all negative with anti-C^w, anti-Wr^a, anti-Be^a, anti-Vw, anti-E^w, anti-Mi^a, and anti-Js, and all 309 type O's were Vel-positive.

COMMENT

The very low incidence of Di^a in the Alaskan Indians was the most interesting finding. This is the only American Indian

population reported to date that has not had at least five per cent Di^a-positive. The northern Athabascans are thought to have been among the last of the Indians to arrive in America from Asia, some authorities dating their arrival after that of some of the Eskimo groups (Jenness, '41). The highest incidence of Di^a so far reported from America has been from South America Indians (Levine et al., '56) with lower frequencies in North American Indians (Lewis, Chown and Kaita, '56; Lewis et al., '56; Chown et al., '58; Allen et al., '58). Diego-positives are found also, though not in high frequency, in Chinese (Layrisse and Arends, '56) and Japanese (Lewis, Ayukawa, Chown and Levine, '56). The gene is also found in Burmese and Dyaks of Sarawak (Colbourne et al., '58), but not in Micronesians (Sussman et al., '58), Polynesians (Simmons, '57), New Zealand Maoris (Lehmann, '58) or Australian Aborigines (Simmons, '57). It was also not found in Europeans (Levine et al., '56) nor Negroes (Junqueira and Wishart, '57). The present finding is consistent with the suggestion that the incidence is highest in Indians who have been separated from Asia for the longest time (Colbourne et al., '58). Further understanding of this problem must await studies on South American Indians and in particular on contemporary Asian groups with whom American Indians may have affinities. The low incidence in Alaskan Eskimos shown in the present study and the complete ab-absence in Eastern Canadian Eskimos (Lewis, Chown and Kaita, '56) is also consistent with this explanation. The observed cline in Diego blood group incidence, if substantiated by subsequent studies, can be explained by one of the following: (a) separate origins for each of the groups, (b) varying degrees of intermixture with other populations, and (c) the operation of selection at different intensity in the different populations. There is not sufficient information to decide which of these explanations, if any, is applicable.

The absence of Js-positives indicates at least no large admixture of Negro genes which could conceivably have been introduced by the crews of New England whaling ships.

The results on the Anaktuvuk P[illegible] kimos agree with those reported fo[illegible] MN, and Rh by Laughlin ('57) w[illegible] his blood group studies in the field[illegible] the exception of the MN system, th[illegible] frequencies of the Anaktuvuk gro[illegible] similar to those of the coastal Eskim[illegible] gesting closer genetic relation to the[illegible] to the Indian groups.

The results for both the Eskim[illegible] Indian groups suggest that admixtu[illegible] Europeans has not been extensive[illegible] is indicated by the low frequenc[illegible] and Fy^b and the high incidence of [illegible] both the Indians and Eskimos. F[illegible] comment should be postponed unt[illegible] lication of other studies from North[illegible] ica, particularly those of Steinberg [illegible] Chown and Lewis.

ACKNOWLEDGMENTS

Collections of specimens in Alask[illegible] facilitated by many individuals and[illegible] cies to whom we are indebted. I[illegible] ticular, Col. H. F. Currie, C. Murra[illegible] F. Milan of the Arctic Aeromedica[illegible] oratory, Ladd Field; M. C. Brewer [illegible] Arctic Research Laboratory, Barro[illegible] Burns Jones of the Hudson Stuck M[illegible] ial Clinic, Fort Yukon; Drs. C. Dott[illegible] C. Hopkins of the University of C[illegible] Medical School and Mr. Patrick O'C[illegible] of the O'Connell Trading Post, Anak[illegible] Pass, Alaska. The participation of [illegible] us (A.C.A.) in the field work in A[illegible] was made possible by a grant fro[illegible] Wenner-Gren Foundation for Ant[illegible] logical Research.

We are very grateful to Drs. Gree[illegible] Layrisse, Mohn, Rosenfield, Sc[illegible] Stern, and van Loghem for gifts of v[illegible] reagents as listed in table 5.

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Diego Factor among Asiatic Indians, Apaches and t African Negroes; Blood Types of Asiatic ıns and Apaches[1]

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apparent restriction of the Diego actor to the Mongoloid peoples (Ley-nd Arends, '56) has provided the pologist with a tool of great poten-efulness in the evaluation of popula-f mixed origin. In order to use this to its full advantage, it is necessary e considerable information on groups origin can with considerable cer-be labelled "mongolian" or "non-lian." The present study, under-as a contribution towards expanding edge of the distribution of the Diego , is concerned with the findings in atic Indians, 108 American Apache s, and 775 West African Negroes.

MATERIALS AND METHODS

tic Indians. All the Indians were ts at the University of Michigan at ne of the study. Forty-four came he state of Bombay, the remaining ne came from other provinces, as ed on the map (fig. 1). All typing vere performed within 24-hours of lection of the blood.

rican Apaches. Specimens were ob-from 108 persons requesting out-t treatment for a wide variety of at the United States Public Health e Indian Hospital at Mescalero, New o, and shipped by air mail to Ann Bloods were tested within 4 to 9 f collection.

persons bled were presumably all its of the Mescalero Apache Indian ation. The total sample, however, eterogeneous as to the tribal origins se persons; that is, on the basis of ents made at the time the blood was there were 47 Mescalero, 23 Chiri-s, three Mescalero-Chiricahaus, 15 s the offspring of marriages between leros and other Indians (among the "other Indian" spouses numbered three Piuma, one Navajo, one Pueblo, one Commanche, 6 listed as Mexican, and two unknown), 11 pure blooded Indians of other tribes (two Choctaw, three San Carlos, one Kiowa, two Lipan, and three listed merely as Apache) and 9 persons the offspring of Indian-Caucasian marriages. The entire group will be referred to as Mescalero Reservation Indians.

Negroes. All African bloods were collected as part of a comprehensive survey in which the bloods were examined for sickling, hemoglobin, haptoglobin, and red blood cell antigen types. This report is concerned with only the tests for the Diego antigen on these bloods. The complete results of the survey will be presented elsewhere.

Two hundred and sixty-two oxalated specimens were received from the Institute of Hygiene, Abijan, Ivory Coast. A little less than half of the total came from 5 tribes: Mossi, 36; Kru, 36; Guéré, 21; Malinké, 18; and Bété, 12.

The second source from which 513 samples were received was the Institute of the American Foundation for Tropical Medicine, Harbell, Liberia. The numbers of samples from tribes from which more than 20 specimens were received were: Webbo, 66; Kpelle, 65; Kru, 43; Loma, 35; Bassa, 30; Gebo, 27; and Gio, 26. One hundred and thirty-eight samples were unidentified as to tribal affiliation.

All specimens were air shipped to the United States in ice packed thermos containers and were tested within 4 to 7 days after collection.

Serums. The anti-Diego serum used was kindly supplied by Dr. M. Layrisse. All other typing serums were obtained from commercial sources, the methods of test-

[1] This investigation was supported in part by a grant from the United States Atomic Energy Commission (project AT(11-1)–405).

ing being as described by the vendor of each particular serum. All tests were performed in tubes with washed 2% red blood cell suspensions, using the antiglobulin method to detect reactions with *all* non-saline-agglutinating antibodies.

In order to conserve serum, a two stage screening procedure, in which only those bloods positive for certain reactions were then tested with other reagents, was used as follows:

Blood positive for	Then tested for
A	A_1
C	C^w, c
E	e (e negatives were retested with trypsinized blood)
K	k

Screening for D^u was performed b ing all bloods negative to saline with a potent incomplete anti-D b antiglobulin method.

RESULTS

Diego antigen. The frequencies Diego antigen among the populatio ported are listed in table 1. The 4 positive Apache bloods came from Mescalero and one "Apache" (trib known). Since the two tribes (Mes and Chiricahua) did not differ signif ly in the frequency of the Diego an (P = 0.28, by the exact 2 ×2 test results for these two tribes as well three Mescalero-Chiricahuas were p to yield a frequency of positive re for the Diego antigen of 4.1%.

Fig. 1 Birthplaces of 75 Indian students at the University of Michigan.

e of the African bloods from the tribe gave a weak Diego reaction was interpreted as either a false positive or a true variant, for in an absorption experiment, this blood failed to remove the anti-Diego activity of the serum when tested against a known positive reactor. The possibility remains that this single positive reaction may have indicated a mutation at the Di^a locus, but because the blood failed to absorb anti-Diego completely, it was scored as negative.

TABLE 1

Frequency of the Diego antigen

	Number	Di^a positive
ns	775	0 (1[1])
lero Reservation ans	108	4 (3.7%)
es[2]	73	3 (4.1%)
: Indians	75	0

e Diego character of one blood was not esolved—see text.

cludes 47 Mescaleros, 23 Chiricahuas, and Mescalero-Chiricahuas. The 4 Di^a positive were from three Mescaleros and one he" (no tribe indicated).

Other blood groups. Both to gauge the representativeness of this material and to extend knowledge on the serotypes of man, other blood groupings were also performed. A comparison of the observed blood group frequencies with those published in Mourant's "The Distribution of the Human Blood Groups" ('54) indicated that these two groups (Asiatic and American Indi-

TABLE 2

Blood group frequencies among American Indians from the Mescalero Reservation, New Mexico, and Asiatic Indians

	Gujarati Indians	Total Asiatic Indians	Apaches[1]	Mescalero Reservation Indians[2]
1	.225	.213	.466	.444
2	.050	.040	.014	.009
	.350	.373	0	.019
	.350	.347	.521	.509
1B	.025	.027	0	.019
	N = 40	N = 75	N = 73	N = 108
IM	.475	.467	.699	.704
IN	.325	.347	.274	.278
IN	.200	.186	.027	.018
	N = 40	N = 75	N = 73	N = 108
+	.800/40	.787/75	.647/34	.574/61
+	.025/40	.013/75	0/73	0/108
y^a+	.775/40	.827/75	.593/54	.690/84
e(a−b+)	.850/40	.760/75	.742/31	.796/49
e(a+b−)	.100/40	.200/75	0/31	0/49
e(a−b−)	.050/40	.040/75	.258/31	.204/49
CDEe	0	0	.014	.029
CDee	.300	.307	.225	.229
^{w}CDee	0	.013	0	0
cDee	.300	.307	.042	.048
cdee	.050	.027	0	0
cDEE	0	0	.028	.019
cDEe	.075	.133	.423	.429
cDEE	.025	.013	.183	.162
cDEe	.075	.093	.070	.076
cDee	.025	.013	.014	.009
cdee	.150	.093	0	0
	N = 40	N = 75	N = 71	N = 105

[1] Pooled Mescaleros, Chiricahuas, and Mescalero-Chiricahuas.

[2] Among the Mescalero Reservation Indians, 72 of the 79 C positive bloods were tested or C^w and found negative.

ans) were acceptable as representative samples. Table 2 presents the findings in the other blood group systems studied.

Of the Asiatic Indians, 40 persons whose parents came from the province of Gujarat to the north of Bombay, were analyzed separately as the closest approximation to a homogeneous group. The majority of the students listing their birthplace as Bombay were Gujaratis so that the Gujarati and Bombay phenotype frequencies will be closely similar. Since information as to caste was not obtained, and it is known that even within the same caste significant differences exist between endogamous groups (Sanghvi and Khanolkar, '50) it was not expected that the sample would be homogeneous; chi squares, however, for the comparison between observed and expected frequencies for the Gujarati, were not significant (ABO, 1.45; MN, 3.52, for both d.f. = 1).

Blood group frequencies for the Apaches were determined from a sample made by pooling Mescalero, Chiricahua, and Mescalero-Chiricahua Indians. The chi squares obtained by the 2 × 2 contingency tables did not indicate between tribe heterogeneity for the ABO, Fy, P, and Rh systems. Chi square for the MN system was significant (6.2, d.f. = 1). The significance to be attached to this observation is not clear and the data are nevertheless presented in the pooled form. The column headed Mescalero Reservation Indians presents the blood group frequencies fo entire group as representative of the calero Reservation area.

Some caution must be exercised i interpretation of the Lewis blood typ the Mescalero Reservation Indians ir the actual presence and size of th (a–b–) class may be an artifact ca by the age of the samples at testi

Blood group gene frequencies fo selected groups, as calculated by methods described by Mourant ('54) presented in table 3.

DISCUSSION

Diego. The findings reported here firm the reports that the Diego antig lacking among Negroes (see Layrisse for a review); however, this is the extensive report on Africans. Layrisse Arends ('57) had examined the blo 107 Africans distributed among 5 t with negative results. Of the 775 Afri tested in the present study, 10 tribes represented by at least 20 members. O possibly, a large proportion of the 138 sons unidentified as to tribal origin were members of the same 10 tribe that each tribe actually is represente a greater minimum number than tha corded. Be that as it may, the size o total sample tested here makes it ce that the Diego antigen does not among native West Africans with reasonably detectable frequency.

TABLE 3

Blood group gene frequencies among Apaches of the Mescalero Apache Reservation and Gujarati of India

System	Gene	Gujarati	Apache		
			Mescalero	Chiricahua	Total[1]
ABO	p_1	.153	.301	.166	.269
	p_2	.040	.014	0	.009
	q	.237	0	0	0
	r	.571	.684	.834	.731
MN	M	.639	.894	.740	.836
	N	.362	.106	.260	.164
P	p	.447	.632	.603	.594
K	k	.987			
Fy	Fy^b	.474	.675	.577	.638
Rh	CDE	0	.025	.046	.015
	CDe	.443	.442	.454	.471
	cDE	.100	.453	.411	.450
	cDe	.029	.080	.089	.064
	Cde	.070	0	0	0
	cde	.359	0	0	0

[1] Includes Mescaleros, Chiricahuas, and Mescalero-Chiricahuas.

ce no positive reactions were found g the 75 Asiatic Indian students, it e safely assumed that the Diego an- at most exists with a very low fre- y among Indians in the Bombay area. ong the Mescaleros, the Diego anti- as a frequency of 3/47 or 6.4%. Be- the numbers are small, the Chirica- were pooled with the Mescalero to a frequency of 3/73 or 4.1%. None e 23 Chiricahau were Di^a positive, e actual status of the antigen among embers of this tribe cannot be es- hed until a larger sample is secured.

er blood groups. Since Sanghvi and olkar have shown that heterogenity between endogamous groups within ame caste, the blood group frequen- resented here for the Gujarati have limited significance; they have been ated to demonstrate the general agree- with those already on record for In- populations.

e Mescalero Apaches (including the alero and Chiricahua) conform to eneral blood group frequencies of the -American Indians described by Mou- ('54), i.e., a high frequency of O) and M (.836) a relatively high fre- y of cDE (.450) and the absence e.[2] Unlike the Fort Apache Indians, ver, among whom the CDE frequency eported to be .125 (Kraus and White, the Mescalero Apache CDE frequency .5.

TABLE 4

erved and expected Rh zygote frequencies among 71 Mescalero Apaches[1]

	Observed	Expected
EE	.000	.0002
Ee	.014	.014
ee	.225	.222
ee	.042	.060
Ee	.423	.426
EE	.028	.013
EE	.183	.203
Ee	.070	.058
ee	.014	.004
	.999	1.0002

cluding 45 Mescaleros, 23 Chiricahuas, and Mescalero-Chiricahuas. Chi squares with egree of freedom are:
hin tribe—Mescalero, 1.63; Chiricahua, 1.21.
veen tribe—Mescalero-Chiricahua, 2.84.
l for the figures reported in this table, 2.98.

There is good agreement between the observed and expected zygote proportion (table 4). A significant difference between the observed and expected zygote proportions among the Fort Apache Indians was taken as evidence for selection, but the Kraus and White Rh typings have been criticized on technical grounds (Chown, '57).

SUMMARY

The Diego antigen was not found among 75 Asiatic Indians or among 775 West African Negroes. The antigen was found, however, on the red blood cells of 4 of 108 Indians from the Mescalero Apache Reservation, New Mexico.

Blood grouping of the Asiatic Indians and Apaches were performed for the ABO, MN, Rh, P, Kell, Duffy, and Lewis. Only limited information can be drawn from the blood groupings of the Asiatic Indians, due to their diverse origins.

The Mescalero-Chiricahua combined gene frequencies were in general similar to those previously reported for American Indians as demonstrated by high frequencies for the genes responsible for the O (.731) and M (.836) reactions, relatively high cDE gene frequency (.450) and absence of the cde gene-complex.

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The anti-Diego serum used in this study was very generously supplied by Dr. M. Layrisse. The Liberian blood samples were drawn under the supervision of Dr. Frank Livingstone, and the Ivory Coast samples under that of Dr. G. Binson. Mr. Peter Kunstadter and Dr. H. E. Sutton cooperated in making the Apache bloods available for this study.

[2] Brown et al. ('58) have reported gene frequencies which differ slightly from those reported here on the basis of these very data. The discrepancy lies in the facts that two samples were discovered to be repeats, bringing the total from 110 to 108 and that more complete tribe information became available enabling the gene frequency calculations to be made for a reasonably pure Apache group, whereas the gene frequencies reported by Brown et al. were computed for the entire group.

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ısplantation Studies of Factors in etal Organogenesis

HE SUBCUTANEOUSLY IMPLANTED IMMATURE G-BONE OF THE RAT AND MOUSE[1]

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purpose of this paper is twofold: to illustrate the application of a : transplantation technique to the of certain processes in the develop- ıeletal organs of the mouse and rat; l, to discuss some observations and ısions that have bearing upon the :al anthropologist's problem of inter- ıg skeletal form and function. We ısed subcutaneous whole-bone trans- not only in the study of skeleto- .s *per se*, but also in the investigation blems in tissue storage and the fate letal tissue grafts or transplants. The ture, growing whole-bone is an inter- and profitable substitute for simple grafts, for deviations from normal ɔgenesis can be used as dynamic a for tissue survival and behavior in 'aluation of storage methods (Felts, or host reaction (Felts, '57b). It is illuminating divergencies, as well as ere existence of the postnatal organ non-functional site, that have re- in our present discussion of fac- ı skeletal organogenesis. The incom- ess of the picture is due largely to ctor of time rather than that of de- or the experiments discussed here are f a continuing series. At the present ı study is being made of the mouse rus grown under controlled longi- ıl compression and the behavior of nbryonic and postembryonic mandib- mplant is under investigation. This should serve to establish certain ses on which these and subsequent ıtations will be made.

he late nineteenth century there was ished a concept of skeletal plasticity and dependency of organization upon the functional environment. A review of this historical development is not warranted here (see Murray, '36 and Evans, '57), but the concept is best expressed in Wolff's Law (1892) which states simply that a given bone is organized to meet a particular functional circumstance and that if the functional circumstance is altered, then the bone's structure will be altered. Conversely, the pathologically altered bone will reorganize to meet again the functional milieu. Although there has been considerable controversy about certain details, the basic tenet is acceptable today, especially as it applies to the advanced or mature skeletal organ.

Almost from the beginning, however, the idea of dependency upon the environment was applied rather in excess to the process of skeletogenesis. It required the development of a new technique—tissue and organ culture—to establish that the differentiation and early development of the skeleton is dependent as much, if not more, upon an inherent pattern than upon functional circumstances. Since the 1920's, Fell and her associates (see summary review in Fell, '56) have studied the skeletal elements of the chick, *in vitro*. It has been shown that any cultured long-bone primordium will exhibit a high degree of developmental autonomy, producing the cartilage model from preskeletal limb-bud mesenchyme. The same is true of any

[1] This investigation is being carried out under grants from the National Institute for Arthritis and Metabolic Diseases, NIH, PHS (A-1104) and the Medical Research Fund, Graduate School, University of Minnesota.

cartilage-preceded skeletal unit. Similar cultures have shown that joints will differentiate in isolation. More recently, mammalian skeletal primordia have been cultured *in vitro* with comparable results (Chen, '52; Ray et al., '54). Long-bone primordia (chick) also have been cultured in the richly vascular chorio-allantoic membranes of the chicken egg (Murray and Huxley, '25; and Murray and Selby, '30) and (rat primordia) in the adult rat brain (Willis, '36).

These studies have led to the conclusion that the general form of embryonic long-bones is the expression of the inherent pattern of development of the skeletogenetic tissue. It may be concluded too that the fine features, superimposed on the basic form, are dependent upon the concomitant differentiation of the functional limb. Murray has summarized these findings as follows: ". . . the gross form of . . . (the) parts of the limb skeleton is developed by self-differentiation, that is, under the direction of factors intrinsic in each developing element. These factors are not, however, sufficient for the production of a functional skeleton. In the early stages, when the development of gross form is progressing, it is doubtless essential that extrinsic forces . . . shall not deviate far from the normal conditions; it would be absurd to suggest that the intrinsic factors could produce a normal skeleton however unfavorable the extrinsic factors might be. In the early stages the intrinsic factors are determinative, the extrinsic factors only important in providing conditions in which the intrinsic factors can act. In later stages, when the gross model is being refined and perfected the importance of extrinsic factors increases." ('36, pp. 19–20).

When one turns from the isolated embryonic rudiment to the postembryonic skeletal organ, he is faced with the rather unexplored problem of the relationship of the inherent, intrinsic and the functional, extrinsic factors in more advanced development. There are several major questions concerning the relative importance of these two groups of factors in the period between the cartilage model, just ossifying, and the mechanically orientated and adaptive calcium storehouse that is the adult bone. For example: Once ossification has how much is morphogenesis depende on, or—indeed—limited by, the forc within the limb? To what degree overall growth process dependent up specific pattern and level of blood su How rigid is the pattern of ossificatio the sequence of primary and seco centers of the organ existing outsi system? Will articular surfaces hold acquired form in the absence of n joint relationships? At a nonpathol whole-organ level, we have little i thing upon which to base answers to and many other questions. By the p technique, however, it is possible proach answers to at least some of questions.

Because of the nutritional and tem limitations inherent in the techn organ culture (*in vitro*) and chorio-a toic grafting are practical for onl very shortest-term experiments with volumes of tissue. The long-term e ment with skeletal organs requires cular site within the body of a hos able of surviving at least as long a duration of the most active phase of g of the implant. As may be seen i following survey, many different si a variety of laboratory animals have used by previous investigators.

The brief literature on postnatal o or major tissue-blocks implanted i mature or adult hosts is colored b fact that only the autologous or isol implant will succeed for more than two weeks. In the currently acce terminology (Transpl. Bull., '55), plants or grafts fall into the foll categories: *autologous*, within a singl vidual; *isologous*, between individu the same inbred strain; *homologou* tween members of the same s (strains differing); *heterologous*, be individuals of differing species. I experiment with the mouse, the im are isologous, the strain (BALB/c) inbred. The rat implants are ac homologous, the animals not being i by current standards. However, ou phalanx implants, between litter-m with parents mated siblings, evid none of the characteristics of the rea seen with our later frank homogra

ıouse (Felts, '57b). In current and :ted studies, however, only the inbred : would be used.

ın and Simon ('23, and Simon and '25) implanted long bones (and ns thereof) of the guinea-pig fetus matures and adults of that species. found essentially normal short-term h of whole bones and longer survival tilages only—essentially the findings cent studies of homologous mouse s (Bacish and Wyburn, '55; Felts, Barnicot ('41), interested primarily genetics of a strain in which resorp- ; sometimes lacking, carried out (isol- , subcutaneous) implantation of rib ents and parts of tibiae between lit- ates. A similar study has been made llette *et al.* ('57). Rib segments and halves (rat) have been implanted elin ('54) in order to evaluate the ı of certain female hormones upon the symphysis. Like Barnicot, he demon- d cartilage growth and the progress sification in ribs and, further, illus- l basically normal morphogenesis in elvis. The study of Willis ('36) dem- ates that the embryonic rat long will develop to postnatal levels in rain of adults.

least two studies of isolated cartilage relation to our chief interest. Du- ıs ('41) investigated the rates of h of autologous and homologous car- (costal, cubed) implanted subcuta- ly in the rabbit. He demonstrated cartilage retains a growth rate directly ve to that expected for site of origin e of donor. In a series of papers cul- ting in a monograph, Lacroix ('51) nly documented the growth behavior physeal cartilage (rabbit) in the renal ıle and brain, but also presented evi- : of the ability of growth-cartilage to e (rather than simply precede) osteo- sis. This aspect is related directly ır own experiments and we will ıpt to elucidate its role in whole-organ opment.

MATERIALS AND METHODS

e experiments reported here consist tially of the removal of a whole-bone the embryonic, neonatal, or im- re mouse or rat and its implantation, intact or in pieces, under the skin of either a litter-mate or an adult where it grows and develops. Unless otherwise indicated, these implants or transplants (the former term best suits the non-functional circumstance and unnatural position) are of the *isologous* type.

The site for implantation, generally termed subcutaneous but actually subpannicular, has been used simply for ease of approach and because, after early trials, no real value could be seen in the use of such relatively difficult sites as the renal capsule or the brain. The immature donor is sacrificed with ether, washed in 70% alcohol and placed under a compound dissecting microscope. The bone is removed with iridectomy scissors and fine forceps and placed in isotonic saline or Ringer's solution while the rest of the group is collected. Although most of the adherent muscle tissue is removed, cleaning is stopped short of possible derangement of the periosteum or perichondrium. The host is ether-anesthetized and a small area on the dorsal lumbar region is cleared of hair and scrubbed with alcohol. From a short midline incision in this area, small scissors are passed in laterally under the pannicular layer to create pockets into which the bones are placed. Care is taken that the implants are as far from the incision as possible and that, if more than one bone is placed on a side, they are not in contact. The incision is closed with sutures and a covering of colloidin. By this technique, some 600 implants of long-bones and certain others of the skull and thorax have been made with only about 5% loss due to infection or (homografts excepted) vascular failure. Only in the case of postnatal mandible implants was it necessary to add wide-spectrum antibiotics to the saline to combat bacteria (a frequently unsuccessful measure).

When removed from the host, implants are fixed in formalin or Zenker's solution, then either processed for sectioning or cleared in KOH (with alizarin red S) and glycerin for gross study. This is a modification of the technique of Noback ('44). Photographs for drawings and measurements are made with an Exacta 35 mm camera (72 mm microtessar lens) on a Varex macrophotographic apparatus with

which single bones are now being studied in serial photographs taken via skin windows (Felts and McCarthy, '58). Other measurements are made on the fresh or cleared specimen with a Zeiss ocular micrometer (vernier dial) mounted on a dissecting microscope.

Because this paper represents a selective summation of results from a variety of experiments, some indication of the numbers of implants and controls is required. Figures 1, 2, and 3 represent results of a long-term study of the rat phalanx implanted in litter-mates at 5 days after birth. Points on the graph (fig. 1) represent the mean of 4, and in two cases, three individual implants or controls, for a total of 160 specimens. The inked frontal views in figures 2 and 3 are average or composite outlines of all such implants or controls for the given date. Figure 5 is again a composite series of drawings of humeral implants, placed in adult hosts at two days after birth. Each represents three implants for a total of 33 in that particular experimental series. In figure 6, the two-day and 30-day normals (a and b) were drawn from single typical specimens fron very homogeneous population whil implants (c and d) of differing e mental treatment were drawn as a c posite of 5 specimens each. Finall figure 7, A and B, the 30-day experim results were constructed from both dimensions and outlines of 5 imp each, from one of the 6 experimental of this type we have made. In rega all these experiments, it has been our sistent attitude that the illustrative t niques are sufficient for the level o cussion and that statistical treatme neither warranted or desirable for present purposes.

OBSERVATIONS

To test the ability of a small, simple bone to grow and develop and be m tained indefinitely in the subcutan site, the phalanx (proximal, second hind-foot) of the 5-day rat was plac litter-mates. Results are illustrated i ures 1, 2, and 3. This particular bone the type having a secondary center a end (proximal) only, and at 5 days i

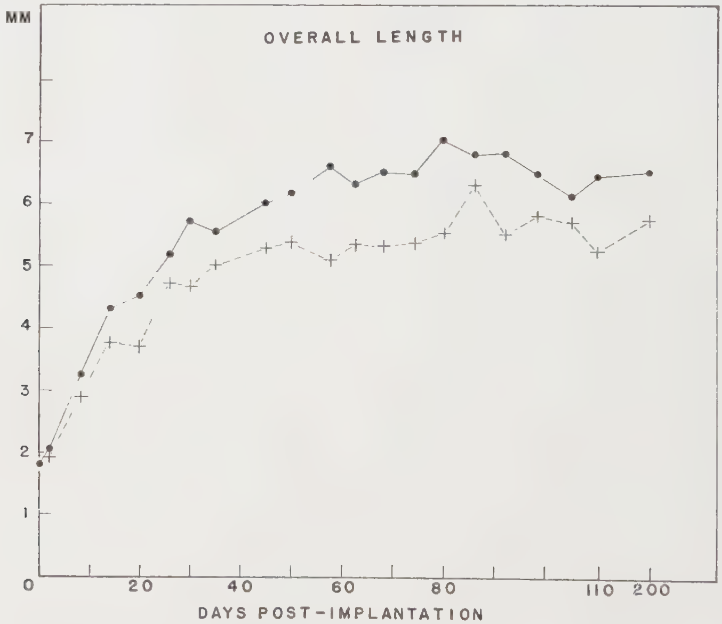
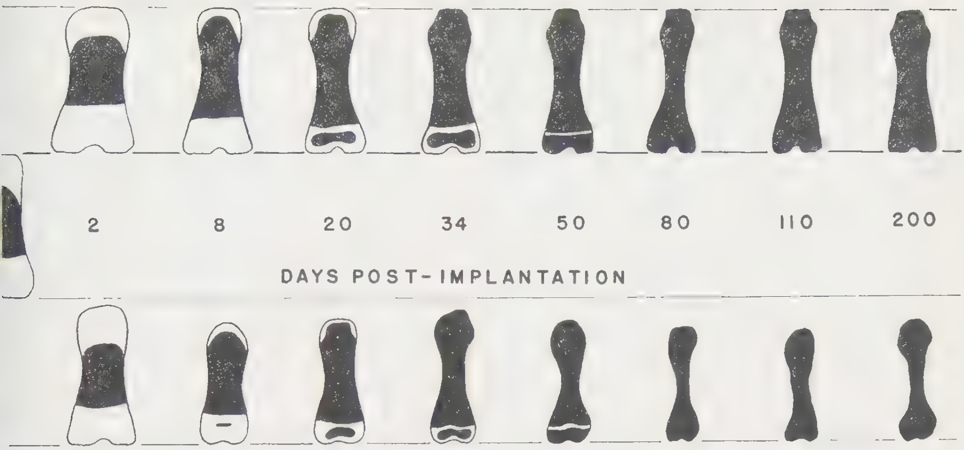


Fig. 1 Growth in length of implanted (broken line) and control (solid line) ra phalanges. Implantation at 5 days postnatal into littermate hosts. Points represent mean of 4 cases each, except for those of 85 and 200 days which are based on only three cases Note compression of horizontal axis between 110 and 200 days.



'ig. 2 Comparison of morphogenesis of implanted and control rat phalanges. Im- ntation (0) at 5 days postnatal. Shaping and the implant/control growth difference emphasized by holding the initial (far left) and all controls to constant height and the plants to correct relative size. Articular cartilage not shown when it cannot be de- ted in scale thickness.

Fig. 3 Comparison of experimental (E) and control (C) rat phalanges at three post- plantation intervals. Articular cartilage not shown where it cannot be depicted in scale ckness. Approximately 5 × natural size.

nately 2 mm in length. Figure 1 de- he growth in length of both implants en line) and controls (solid line). a slight retardation in rate, the curve plants still approximates that of the ls. Final length attainment, 3× the , compares well with that of the con- 3.5×. Overall length is, of course, nction of longitudinal proliferation tilage alone. Morphogenesis is an- and more complex matter.

ure 2 illustrates comparative morpho- s and maturation with initials and ls drawn to common length. In such nat, implants appear progressively shorter because of the lessened rate of growth. Three stages of this series are drawn to scale in figure 3. Relative to these illustrations, the following comments seem pertinent: (1) Maturation, as indicated by the progress of ossification (proportion of ossified shaft to cartilage, size and shape of secondary center), is the same in the two series. (2) The phalanx normally becomes more slender with time. The ratio of proximal and distal diameters to overall length progresses about the same in the two series. Because the experimental becomes flattened in prolonged implantation, the anteroposterior and transverse

diameters had to be averaged to show this. (3) The implant, especially after maturity is reached, undergoes a notable relative and, in many cases, an absolute reduction in mid-shaft diameter. (4) There is a progressive loss of specific or normal details of articular surfaces and shaft form.

Similar results are seen with implantation of young mouse humeri in adult hosts. Figure 6a illustrates the normal two-day humerus, b the normal 30-day, and c the humerus implanted at two days and removed 28 days later. Size attainment of the implant is excellent and maturation is identical with the normal. With implantation in an adult host, the humerus does not revascularize as rapidly as the phalanx does in the litter-mate, and, therefore, lags a bit during the first two weeks. The proximal and distal center normally appear, nearly together, at 5 or 6 days postnatal. In the implant (fig. 5), the distal center only is visible by about 10 days. By 15 days (fig. 5) the implant is essentially normal in ossification. Thereafter the condition of the primary and secondary centers is normal and all subsequent fusions are on schedule. The total development of the humeral implant is shown in figure 5. This series exhibits a loss of small surface features similar to that seen in the phalanx. Note too that the humerus, like the phalanx, has a diminution of shaft diameter after growth is completed.

The environment of the implanted skeletal organ. The environment into which the subcutaneous implant is introduced may be discussed under two headings: nutritional and mechanical. The first involves the re-establishment of a blood-supply to the implant and because of the intricate relationship of this event to growth and development, it is worth detailed scrutiny. The second is relatively simple and rather justifies use of the term "non-functional site."

In its normal position, the skeletal organ is integrated with a specific vascular pattern that differentiated with it (Harris, '28; Weinmann and Sicher, '47; Streeter, '49). In a very real sense, much of the structure of the normal skeletal organ (e.g., marrow-cavity, nutrient foramina, Haversian systems, cartilage canals, and even the organization of the epiphyseal plate) is

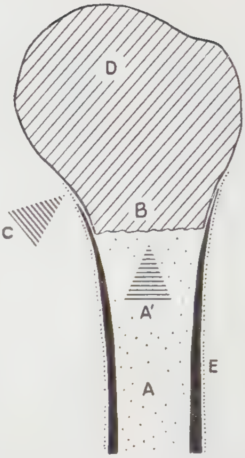
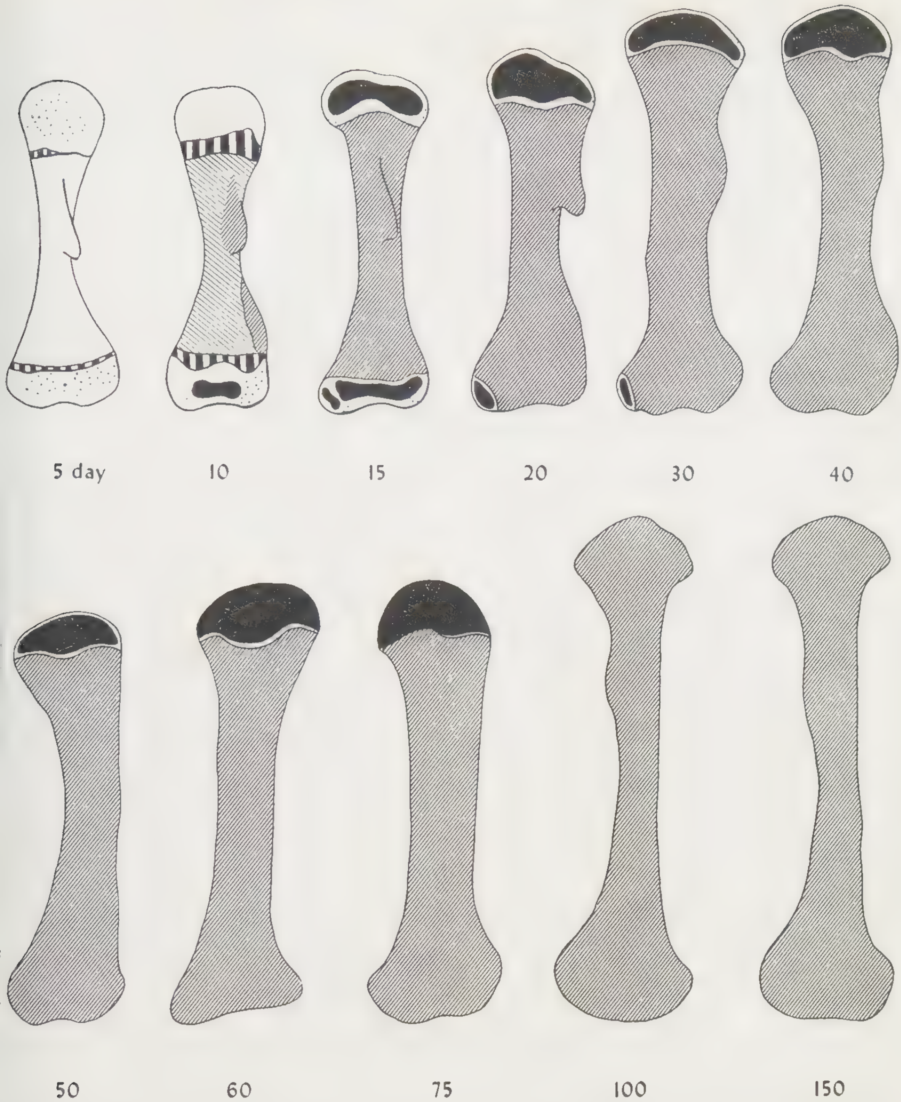


Fig. 4 Diagrammatic representation o[f proc-]
esses and events in the revascularization [of im-]
planted mouse humeri. See details in text.

directed toward a fine dependent re[lation-]
ship with the vascular system (Ham[...]
Harris, '56). It is hardly conceivabl[e that]
the intrinsic vascular pattern, even [of the]
simplest developing long bone, would [con-]
nect end-on with the non-specific ex[...]
pattern of the subcutaneous site. The [proc-]
ess of revascularization is thus o[ne of]
adaptation of a pre-existing osteog[enic]
mechanism to a new vascular pattern[. Fig-]
ure 4 illustrates the sequence of eve[nts as]
they would occur in the proximal e[nd of]
the humerus with the ingrowth of [...]
vessels. The description is based o[n the]
blood vessel pattern observed at im[plant]
removal, and on a correlated analy[sis of]
gross and microscopic distribution of [osteo-]
genesis in implants. Cartilage, with i[ts low]
metabolic demands (Laskin and S[...]
'53), survives transplantation better [than]
the other skeletal tissues. With min[imal]
nutrient supply this tissue block wil[l con-]
tinue transverse and longitudinal g[rowth]
(Felts, '57a). Elongation adds to the [zone]
of hypertrophy of the growth car[tilage]
(fig. 4, B) which is due to be replac[ed by]
bone and marrow. If marrow (A) su[rvives]
the vascular disruption, its osteoge[nic and]
cartilage-erosive component (A') w[ill in-]
vade that zone (B). However, if [revas-]
cularization is tardy or the marrow fo[r some]
other reason fails to survive, then vas[cular]
connective tissue (C) peripheral to th[e im-]
plant will invade the cartilage. This [proc-]
ess occurs in nearly all implants, in i[...]



'ig. 5 A series of mouse humeri, implanted at two days postnatal and recovered at icated intervals. Code as follows: cartilage, stipple; unfused secondary centers, black; ginal bony shaft, white; light deposition of periosteal bone, light diagonal; heavy deposi- n, dark diagonal. Broad vertical lines indicate region or peripheral invasion of cartilage early stages. Articular cartilage not shown where it cannot be depicted in scale ckness. 8 × natural size.

tion to the activity of the original v. The result, as it usually appears s preparations, is seen in the 5- and implants in figure 5, at either end shaft (heavy vertical lines), and in 3 in histological section. After about s these regions are masked by the n deposition of periosteal bone (see rest of series in fig. 5, and in fig. 9). The most obvious and complete result of invasion from the periphery is seen in figure 6 (d) under circumstances which will be described in the next section. The invasive process just discussed is virtually identical with the intrusion of osteogenetic vascular mesenchyme into the central zone of cel-

lular degeneration and matrix calcification in the early cartilage model (Barnicot, '41 and Streeter, '49).

Two other events in the process of revascularization are of importance to the morphogenesis of the implanted long bone. The first postimplantation activity of the periosteum (fig. 4, E) is the production of a layer of cartilage, not bone. This thin cartilage, invisible in cleared specimens but obvious in histological section (fig. 10), is subsequently replaced by a layer of bone trabeculae which are observable (fig. 5, 10-day and fig. 11) as a light deposit of new bone. Thereafter, bone deposition progresses on the trabeculae but the cortex is thus spongy—like a fracture callus—for a considerable period. The final result is a heavy, uniform layer of bone (fig. 5, 19-day and beyond and fig. 12). The entire sequence is comparable to callus formation in experimental fractures (Ham and Harris, '56) and is indicative of the bipotency of skeletogenetic cells under trauma or vascular disruption (Lacroix, '51). Lastly (fig. 4, D and fig. 11), the secondary centers in long-bone implants may arise from invasions in through the articular surface. Such centers (whether originating along one or the other line) may ultimately increase in size until areas of articular surface are replaced.

The importance of revascularization timing, and—indirectly—the role of vascularity in skeletogenesis, is shown vividly in an incidental experiment in which a needle was inserted under the skin and passed around one end of a humerus one week after implantation. At the end of a month, the one end of the humerus had the expected maturity while the other, with disrupted revascularization, was two weeks retarded. Similarly, the age of the host—as related to general connective tissue activity and blood-vessel growth—is an important factor in revascularization. The phalanges grown in litter-mates evidence little or no retardation in maturation (fig. 2) while humeri implanted in adult hosts lag during the first two weeks but finally compare well with controls by one month (fig. 6, b and c). In this regard, the most favorable environment into which we have placed mouse long bones is the highly vascular chorio-allantoic membranes o chick egg. Such implants, practica cause of the immunological immatu the chick embryo, show no lag in ma

In its position between deep muscu and overlying panniculus and skin, t plant is subject to a certain unde amount of compression. This is fested in the anteroposterior flatten the advanced phalanges and in hum planted over 40–50 days. Early in investigation it was considered th velopment of a thin connective t sheath or capsule about the implan expected result of the healing process) might act to retard elongation. In ve the relatively tremendous compre stress we now know to be required tort the cartilage masses of the hu implant (current studies of Monso Felts, abstracted, '58), this view ha rejected.

The behavior of isolated componen long bones. We have examined the gr and development of the implanted bone and discussed the relationshi a new blood supply to the several ponent tissues. The fact that car bone, and their germinative tissues o at different physiological levels and precise spatial relationships permits go a step further and separate the gr components from one another. W thus visualize more clearly the r interrelation of the tissues in the de ing organ.

Figure 6 illustrates 4 humeri o mouse. Specimen a is a normal tw humerus, b is a normal 30-day. Hu c is also of 30 days but spent 28 day subcutaneous implant in the adul stated earlier, its developmental le basically that of the normal but smaller. Specimen d is the same age but after the donor was sacrificed a days, the body was stored at 24° f hours before the humerus was imp for the standard 28 days. This tem ture and duration of storage has found to be sufficient to permit only lage to survive (Felts, '57a). Bone osteum, and marrow, with higher met demands, were subtracted from the g pattern. The cartilage grew and its e

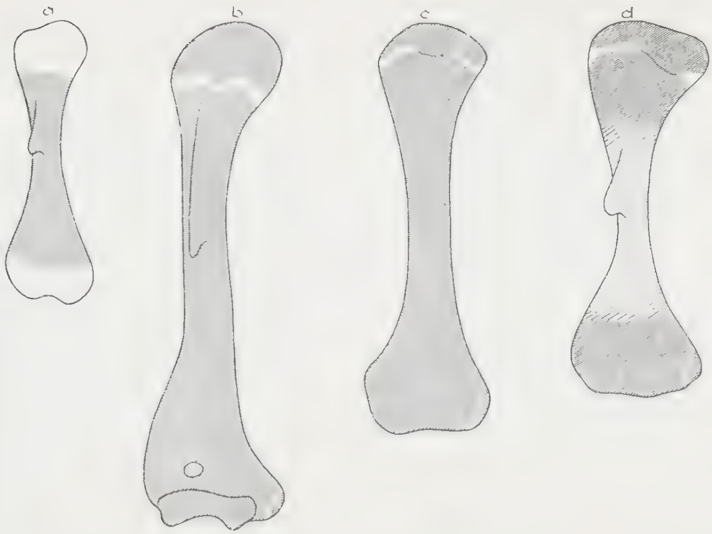


Fig. 6 Comparative series of control and experimental mouse humeri. Specimen a is a ›rmal two-day postnatal; b is a normal 30-day. Specimen c is an implant of the same ;e (two days plus 28 days implantation). Humerus d is of the same timing as c, but as stored for 24 hours at 24°C. Code: cartilage, white; all vital bone, dark diagonal; ›ad bone, stipple; composite on d, overlap of vital on dead bone. Articular cartilage ›t shown where it cannot be depicted in scale thickness. Approximately 8 × natural size.

vas replaced by bone and marrow de- from the invasion of peripheral vas- connective tissue. The result is a lete marrow-filled metaphyseal os- attached to either end of a (two-day) shaft (fig. 13). At the distal end, yseal closure is complete while, at the mal end, cartilage is reduced to an yseal line capped by a secondary r covered with articular cartilage. rational status is thus wholly compa- with that of the control implant and al. Actually, the stored humerus is across the ends relative to length is the normal. It has been a consis- observation that with complete lack e intramedullary ossification route, ation is slower but, because of the iate peripheral circulation, consider- transverse growth occurs before os- tion.

e same basic process is seen in the ving experiments in which the carti- and bone portions of a long-bone were n separately in the subcutaneous site. e first (fig. 7,A), the two-day humerus sectioned at the proximal chondro- us junction and the major and minor parts were implanted on opposite sides of the adult host. After a month, the isolated proximal cartilage is seen to have a normal secondary center and to have elongated. The replacement of this elongation by bone has created an upper shaft segment of essentially the shape and size one would find in the intact implant of the same age. The rest of the humerus fared as well. The distal secondary center appeared and then, as expected, fused with the shaft. Before this transpired, however, cartilage elonga- tion added to the length of the segment. New bone also was deposited on the shaft. It should be observed that, while the orig- inal shaft and marrow is absent, the cut surface of the proximal cartilage (i.e., the two-day "epiphyseal line") is directly ex- posed to vascular connective tissue. This contrasts with the condition just described for the stored humerus, and the severed cartilage mass therefore produces a more normal shape than does the cartilage mass isolated atop a dead shaft.

In the second experiment, both carti- lages were freed from the shaft (fig. 7,B). The proximal segment fared as before. The distal is seen to have produced a bit of

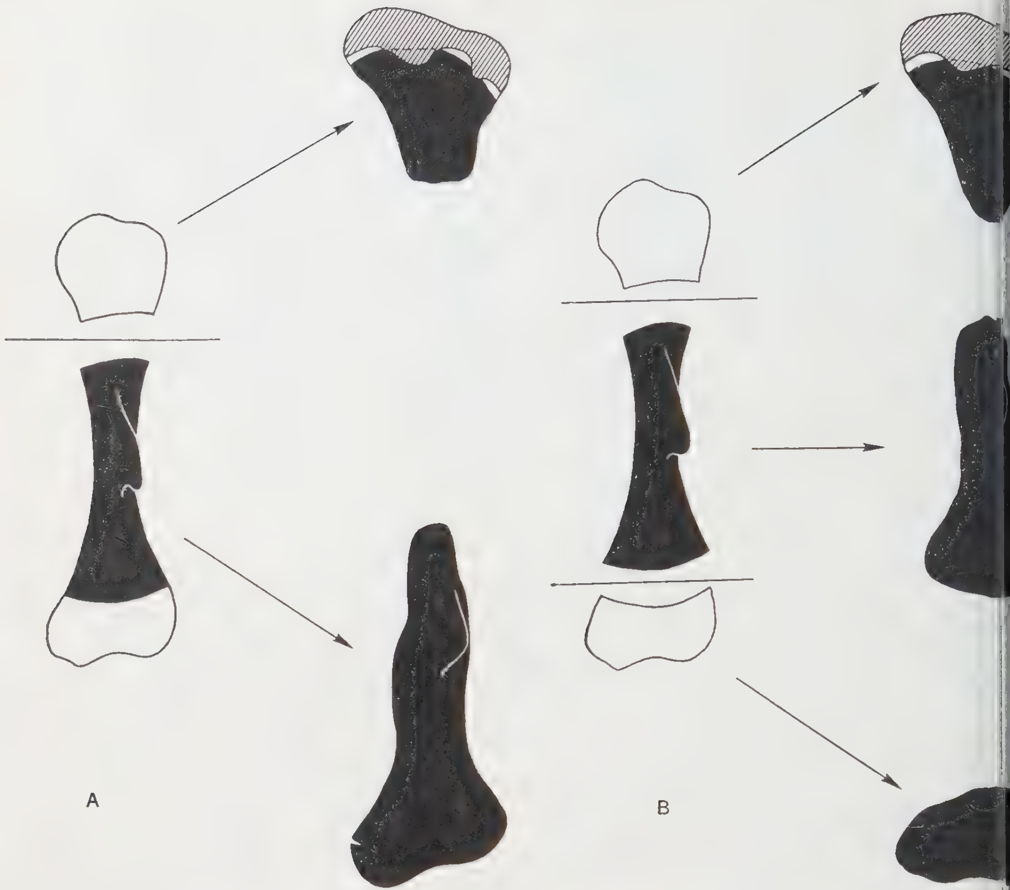


Fig. 7 Results of separate implantation of one cartilage and the rest of the humeru (A) and both cartilage and the isolated shaft (B). Implantation at two days, recover after 28 days. Articular cartilage not shown where it cannot be depicted in scale thick ness. 11 × natural size.

shaft and then the secondary center and the new shaft rudiment fused. Except for a thin layer of bone replacing the narrow zone of cartilage left with the shaft when cut, the middle segment shows no length increase. Diameter was augmented by new periosteal bone.

DISCUSSION

The present experiments clearly illustrate the utility of whole-bone transplantation in the analysis and more lucid visualization of some of the basic skeletogenetic processes. Subcutaneous implantation of immature long-bones is relatively easy, and the host environment is generally adequate for the physiology of the organ and its components. Although the degree of tion does not approach that obtaine *vitro*, the implant is effectively rem from the level of forces encountered i active limb. Actually, the immature bone is as isolated as its relative size cellular composition permit, and int tion into the circulatory system of the permits a vastly greater approximati normal growth rate than does the nut level of *in vitro* culture media. At th sue level, our findings are in keeping the basic observations of earlier (c investigators in bone and cartilage t plant behavior.

The long-term study of the rat pha and the mouse humerus establishes th

ideal circumstances of revasculariza- the immature long-bone will con- growth and development. It appears ne disruption of the original blood and the lapse of time before com- revascularization are enough to ac- for the observable growth insuf- y. The absence of limb conditions, ll that this implies, seems therefore of insignificant consequence to gross ogenesis of the postembryonic long- If one sums up this finding with f Fell ('56) on development of the ge model *in vitro*, it is obvious that— hout development—the general fea- of long-bone size and shape exhibit a of dependency on the mechanical nment.

ough general size and shape develop- n the implant compares so well with ormal, the contrary is true for the pment and maintenance of small ional characteristics." In the pha- normal flatness of the posterior aspect e sharp concavity of the proximal ar surface soon disappear (figs. 2, the humerus, the spine and details articular surfaces are soon absent, ne lateral (supraepicondylar) ridge e olecranon foramen fail to appear 5, 6). These highly specific char- tics of the individual long-bone are sort that fail to appear in *in vitro* es and chorio-allantoic grafts (Mur- 36, summarizing the early work of d colleagues and his own work with y and others). In our subcutaneous nts (humerus), a comparable in- is the absence of the olecranon en. Normally appearing in the first eeks after birth, the aperture is re- to the development of full range of n in the elbow joint. In similar n, the ridge above the lateral epi- le (fig. 6,b) is not yet formed at two and, in the absence of the muscles ing to it, does not develop in the im- However, many of the surface de- are already established in cartilage e at the time of implantation. The cation or disappearance of these re- another explanation.

plants removed at close intervals (as re 5 and in current work with daily photographs) show that the disappearance of protuberances, ridges, and depressions is solely the function of the normal incremental processes of cartilage and bone. The precise features of the original shaft are literally submerged in new periosteal bone, much as the exact form of a figure is lost as it is dipped many times in paraffin (observe the spine across series in figure 5). On the cartilage surfaces, the concomitant loss of characteristic detail must be attributed to the multiplication of cells in the absence of those articular-surface relationships that normally modulate a well controlled, but gross, volumetric increase. There is no evidence, in histological sections, that a germinative perichondrium forms on these surfaces (where it would not normally be present), causing submergence of surface detail.

The gradual loss of characteristic surface detail during active growth is to be contrasted with the fate of attained (implant) form after full maturation is reached. The first we have attributed to the addition of substance without specific functional directive, and resorption is not held to be a factor. However, attention has been drawn twice (phalanx and humerus) to reduction in shaft diameter as a feature of fully grown implants. The developmental end-point is essentially the same in control and in implant, yet reduction of diameter is seen only in the latter. Reduction of shaft diameter is a relative thing. In some humeral implants this dimension is greater than in controls of the same age, and a high degree of individual variation is seen in any series (fig. 5, 5 through 75 days). Such variation is definitely related to the timing of revascularization and, quite likely, to lack of control in the absence of normally circumjacent muscles. Diameter may, incidentally, appear larger in frontal view of specimens that are somewhat flattened anteroposteriorly. The fact remains, however, that many of the humeri are narrower in midshaft after epiphyseal union than are specimens collected earlier (regardless of whether earlier humeri are thicker than normal) and a number of these are narrower than the initial two-day implant. Recently we have observed narrowing of

individual implants followed serially over long periods in skin-window photographs. Finally, fully grown phalangeal implants are almost invariably narrower than were the original 5-day implants. Clearly, this phenomenon requires further study. From the information at hand, however, it might be theorized that after completion of growth, skeletal organ form is maintained in balance with postural and muscular forces, and that absence of these forces in the case of the implant removes the causative factor in form maintenance. One would hesitate to term this "disuse atrophy" because of the long delay and apparently precise onset, and because of the absence of general rarefaction of bone.

We are in agreement then with Murray's contention that the gross form of long-bones is determined by intrinsic factors while specific details and precise relationships with other skeletal units are determined largely by active and passive components of the normal limb. However, we would extend the period of development encompassed by Murray to include the total organogenesis of the long-bone. Further, we would suggest the possibility of a need for the functional environment to maintain that which, ontogenetically, may be produced in comparative disregard of it. There remains but to define, in terms of these results and the available literature, the nature and extent of the intrinsic factor.

The intrinsic factor responsible for the high autonomy of long-bone development is obviously the nature of the cartilage model. In the general literature, "cartilage model" usually implies simply a miniature of the future "bone," differentiated from mesenchyme and not yet subjected to osseous replacement. In terms of total development—as analyzed by *in vitro* cultures, chorio-allantoic grafts and *in vivo* implants—the cartilage model may be defined more broadly as a pattern or format which expands by its own means and upon which the total organ is constructed. Transplantation studies demonstrate that long-bone development is more than a series of coincidental temporal and spatial relationships of cartilage and bone. Lacroix ('51) implanted the isolated central portions of epiphyseal cartilages into the brain and renal capsules. These im[...] were free of perichondrium, perio[...] and marrow, yet endochondral ossifi[...] was re-established and bone formed [...] periphery, just as the edge of the m[...] shaft constantly overlies a portion [...] growth cartilage. Lacroix interpret[...] result to mean that cartilage induce[...] differentiation of bone *de novo*. I[...] plants of whole isolated proximal and [...] humeral cartilages, we have seen bo[...] place cartilage where and when it [...] have in the intact organ. With c[...] minor differences, the same process [...] in the cartilage of stored humeri. [...] ested as we are in morphogenesis [...] than cell differentiation, it is not [...] diately pertinent whether the osteog[...] tissue arose from the perichondrium [...] implanted cartilages or from stim[...] osteogenetic-potential cells in the hos[...] Lacroix's implants and these cart[...] point to a process by which growth [...] maturation in the cartilage model c[...] osteogenesis in the skeletal organ. [...] autonomy of development in the car[...] preceded skeletal organ is, therefore [...] expression of the pattern of differ[...] growth and maturation rates and [...] tions established at the differentiati[...] cartilage from limb-bud mesenchym[...] the same time, local compressions [...] tensions set up in the limb enviro[...] are reflected in the development and [...] tenance of surface detail. This patt[...] operable in the highly resilient car[...] model and, with ossification, in all th[...] divisions of the model, until static [...] ular cartilage alone remains. Ossific[...] is but a continual process of substi[...] of highly plastic osseus tissue into a[...] panding pattern derived from the e[...] onic cartilage model. This cartilage [...] is the determinate of size, gross shap[...] maturation. Within broad limits of n[...] mechanical, nutritional and hormon[...] fluences it is essentially self-governi[...]

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PLATE 1

EXPLANATION OF FIGURES

8a and 8b Two photomicrographs illustrating early (a) and advanced (b) stages of endo-chondral ossification in the proximal end of the implanted mouse humerus. Implanta-tion at two days postnatal, removal at 7 and 14 days respectively. Note early invasion of cartilage, by-passing the original ossification front. In later specimen, a basically normal epiphyseal growth zone is established. Original cartilage front and an island of earlier cartilage remain and are partially covered by bone. × 28.

9 Photomicrograph of upper half of ossified shaft of 16-day implanted mouse humerus, illustrating uniform deposition of trabecular bone resulting from replacement of early post-implantation formation of cartilage by periosteum. Some atypical endomedullary trabeculae are also visible. × 28.

10 Section through upper half of ossified shaft of 6-day implanted mouse humerus, illus-trating formation of cartilage by periosteum of humeral spine. Note invasion of cartilage and partial replacement by bone and marrow. × 28.

11 Section through proximal end of implanted humerus of 21 days. Epiphyseal growth cartilage is of normal appearance. Secondary center is well-developed but articular cartilage is generally absent. × 34.

12 Higher magnification (× approx. 100) view of compact bone eventually formed by de-position on the trabeculae seen in figure 9. Section is oblique through upper shaft.

13 Photomicrograph of frontal section through proximal half of mouse humerus stored 24 hours at 24° C before implantation. Initial age, two days; duration of implantation, 28 days. Original cartilage front represented by transverse bony plate. Marrow to left is as expected; to right it is replaced by fibrous tissue. Diaphysis to right is acellular. Condition of epiphyseal plate is as in unstored implants of same age. × 11.


8a
8b
9
10
11
13

rical and Non-Metrical Features of the Clavicle ne Australian Aboriginal

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rough the craniology of the Austral- boriginal has been extensively stud- re there has been little reference to mainder of the skeleton. This study with the clavicle and the material ned was from the Murray Black Col- n in the University of Melbourne. collection was obtained from a rela- localized area in the South East of alia and the bones used were of n sex.

MATERIAL AND METHODS

m the series available for study, no ion was made other than the state e bone itself. Those bones which d any evidence of pathology, trau- or otherwise, were excluded, and al- ose which were unduly damaged. all, 292 clavicles were examined, of 170 were male and 122 were female. e total number there were 65 pairs les and 45 pairs of females.

e technique used for measuring the was based largely on that adopted by ns ('16), but his methods were not exclusively. Each bone was traced e dioptograph, so that a tracing was ned from above and from the front, vo tracings being as near as possible ht angles to each other (figs. 1 and rom the dioptographic tracings, the ing measurements were made.

The maximum length of the clav-

The distance between the mid of the sternal and the acromial of the bone.

Y) The angulation of the clavicle. ngle of the inner and outer ends and tal angulation of the clavicle were obtained according to the method outlined by Parsons.

(3,4,5) The length of the segments. The lengths of the three segments were recorded as by Parsons.

(6) The width of the inner end.

(7) The width at the inner angle.

(8) The minimum width and

(9) The distance of this point from the mid-point of the inner end.

(10) The width at the conoid.

(11) The maximum width of the outer end.

(12) The height of the inner end.

(13) The height at the mid-point of the bone.

(14) The height at the conoid.

(15) The minimum height of the outer end.

Several of the above measurements could also be made directly on the bone, such as: The maximum length, the width of the inner end, the minimum width, the width at the conoid, the width of the outer end, and the 4 measurements of the vertical height. As was to be expected, there was, on occasions, a minor discrepancy between the measurements made on the tracing and those made directly on the bone. In all cases where such a discrepancy existed, the direct measurements were repeated and adopted in preference to those made on the tracing. In addition, the circumference of the clavicle at its mid-point was directly measured with a steel tape.

In the majority of cases, the corresponding humerus was also available for measurement. The maximum length of this bone was recorded and the claviculo-hu-

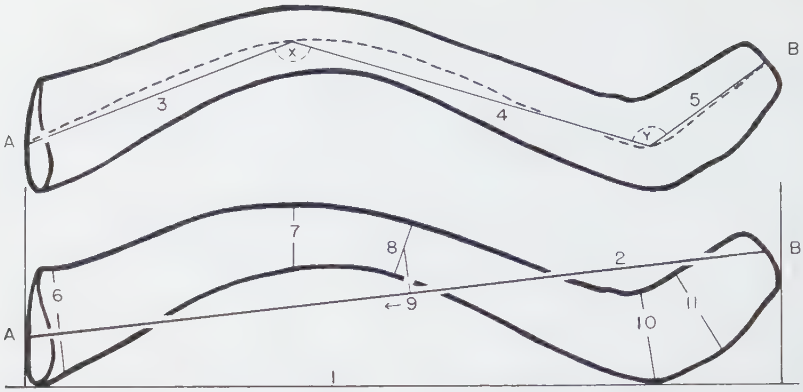


Fig. 1 The measurements as taken on the dioptographic tracings (vertical view).

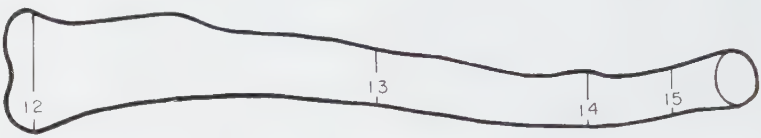


Fig. 2 The measurements as taken on the dioptographic tracings (horizontal view).

meral index thus obtained. Other clavicular indices obtained were:

(i) the thickness index = $\frac{\text{circumference at mid-point}}{\text{maximum length}} \times 100$

(ii) the index of the outer end = $\frac{\text{width of outer end}}{\text{maximum length}} \times 100$ and

(iii) the index of the inner end = width of inner end + height of inner end.

RESULTS

In some clavicles it was not possible to obtain all measurements so that the number of specimens for each measurement varied between 75 and 85 for the male right, 65–75 for the male left, 59–64 for the female right and 54–57 for the female left. This range applied also for the indices except the claviculo-humeral index where the figures were 69, 57, 52 and 46 respectively. The results obtained are summarized in table 1.

Discussion metrical features

Maximum length. In the male the left clavicle was, in the mean, just over 1 mm longer than the right while in the female this difference was just under 2 mm. While the difference is not great, it is interesting to note that in the English the male left clavicle exceeded the right 2 mm whereas the figures for the two in the female were identical. In the A can Negro, (Terry, '32) the male lef ceeded the right by about 1.5 mm the difference in the female was jus der 1 mm in favor of the left side. Fo mean, the left clavicle is, therefore the same length as or greater than right in the Australian Aboriginal as as in the American Negro and the Eng On both sides the mean for the male considerably greater than for the fe There was, however, a considerable lap as may be seen in the frequency tribution graphs shown in figures 3 a In comparison with the English, the W American and the American Negro clavicle of the Australian is shorte between 1 and 2 cms.

The distance between the mid-poin the sternal and acromial ends. There only a slight difference between the sides in the male with the left bein excess of the right. In the female same could be noted but to a greate gree. The mean for both sides in the was greater than in the female wi greater range in the male, the lower being, however, the same in both se

TABLE 1

The metrical features of the Australian clavicle

Measurement	Male						Female					
	Right			Left			Right			Left		
	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
Maximum length	114–158	139.5	9.3	109–160	140.7	9.3	106–139	123.5	7.3	109–140	125.1	7.1
Sternal-acromial distance	106–154	135.2	9.6	108–158	136.0	10.2	106–138	120.6	7.5	108–140	123.2	7.2
Inner angle	139–162	149.9	6.7	137–161	149.0	4.5	138–158	149.3	4.2	142–160	150.8	4.4
Outer angle	120–155	140.8	7.0	123–159	143.8	6.7	122–160	140.8	7.7	128–166	142.8	8.2
Total angle	264–313	295.5	8.5	262–315	293.0	9.2	266–314	290.0	10.2	270–316	293.7	10.6
Inner segment	30–55	43.5	6.0	29–55	43.5	6.1	26–48	36.1	5.1	22–49	38.1	5.7
Middle segment	50–89	70.0	7.0	52–86	68.8	6.1	49–75	63.7	5.2	54–78	63.7	4.9
Outer segment	20–39	27.9	3.7	20–40	30.6	4.3	21–35	26.6	3.1	20–37	27.2	3.4
Circumference	30–48	38.5	3.9	30–46	37.1	3.3	28–40	32.1	2.7	26–41	32.2	3.4
Inner end width	15–28	22.1	2.4	16–29	21.4	2.4	13–28	18.6	2.7	12–28	18.2	2.6
Inner angle width	9–19	13.5	1.7	9–17	12.9	1.5	8–15	10.9	1.5	8–13	10.6	1.2
Minimum width	9–16	12.2	1.3	9–15	11.8	1.1	8–13	9.8	1.2	7–12	9.7	1.2
Distance	14–88	54.1	19.2	18–87	54.2	18.9	17–81	30.9	16.8	16–74	43.2	16.3
Width at conoid	10–22	16.6	2.4	11–20	15.4	2.0	10–20	14.0	2.1	9–20	13.7	2.4
Outer end width	13–30	21.1	2.9	15–27	20.4	2.9	13–28	18.1	2.8	12–27	17.8	2.7
Inner end height	17–28	22.7	2.5	15–30	23.1	3.0	15–27	20.4	2.6	15–25	20.6	2.4
Height at mid-point	9–15	11.4	1.4	7–14	10.6	1.4	7–17	10.1	1.8	7–19	9.9	2.8
Height at conoid	8–15	11.3	1.6	8–16	11.1	1.6	8–14	9.9	1.3	7–14	10.2	1.5
Minimum height at outer end	7–12	9.2	1.2	6–12	8.6	1.3	5–10	7.6	1.0	6–9	7.3	0.9
Claviculo-humeral index	36–46	42.4	2.2	37–48	43.2	2.0	36–46	40.4	2.1	38–47	41.8	1.8
Thickness index	21–39	27.7	3.0	21–32	26.4	2.4	22–31	26.0	2.1	20–34	25.8	3.1
Index outer end	10–22	15.2	2.2	10–20	14.7	2.2	10–21	14.8	2.4	9–27	14.6	3.4
Index inner end	35–54	44.9	3.8	35–57	44.8	4.7	30–51	38.8	4.5	28–49	38.5	4.0

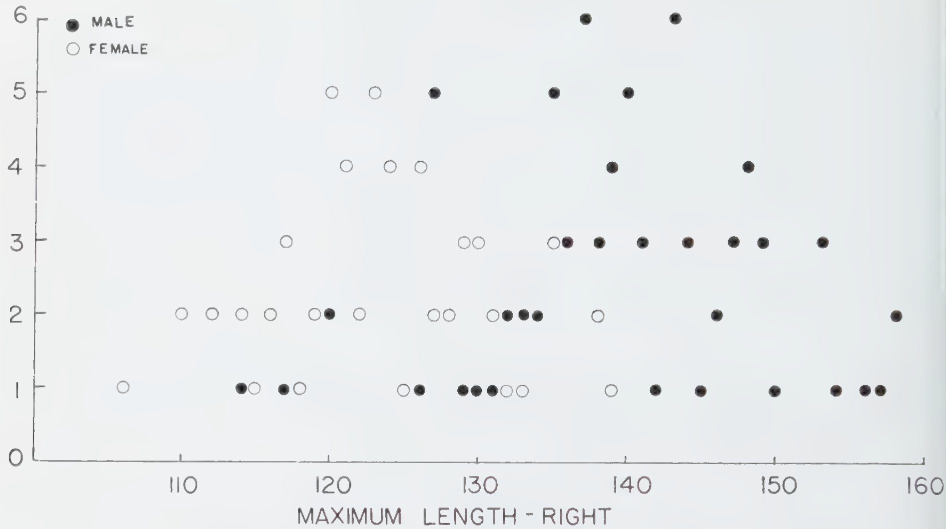


Fig. 3 Frequency distribution of the maximum length (right side).

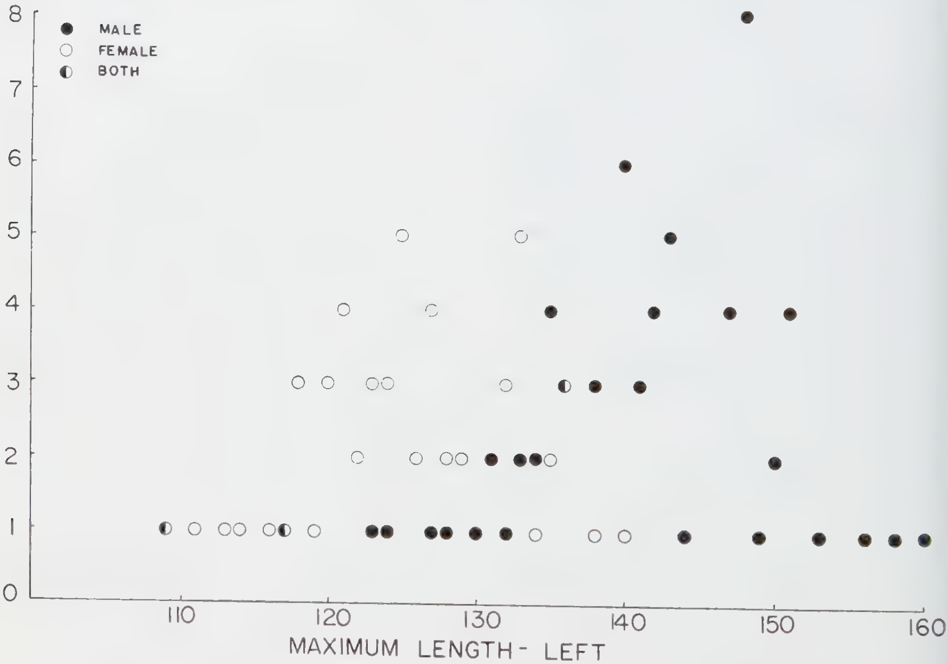


Fig. 4 Frequency distribution of the maximum length (left side).

Degrees of curvature. There is little real difference in the total degree of angulation on the two sides in both the male and the female and little difference between the sexes. The angulation is very close to that found in the English, the American White and the American Negro.

Lengths of segments. The length of t segments in the male exceeded the c responding measurements in the fema In comparison with the English clavi the lengths of all segments are less in t Australian, a feature more obvious in t inner and outer segments.

cumference at mid-point. In the the circumference at the mid-point e right clavicle was almost 1.5 mm cess of the left, while in the female was virtually no difference. For both ight and left sides the male clavicle larger than the left. Racially the alian clavicle was a little less in cir-erence than those examined by Par-and Terry.

e widths of the clavicle. In the male ridth of the clavicle at all points was er, in the mean, on the right side. one exception, however, this differ-was less than 1 mm and in the ex-on the figure was just over 1 mm (at onoid). In the female the same fea-in favor of the right side was shown in all instances the difference was than 0.5 mm.

e distance of the minimum width the sternal end on the two sides ed a difference of only 0.1 mm in the and 2.3 mm in the female. In both the distance was greater on the left In all instances the figures for the s were higher than for the females. lly the figures for the Australian were than those of the English except in nale where the Australian is greater e inner angle and in the minimum 1. This difference, however, did not ed 1.5 mm.

e heights of the clavicle. The 4 meas-ents taken for the heights of the cle are, for all practical purposes, the for each side in both the male and emale and in all 4 measurements the bones were larger than the female. ally the heights in the Australian are at all points than in the English clav-

Indices

e claviculo-humeral index. In the the index for the left side was slight-eater than on the right and even more r the female. On both sides the index the male was greater than in the le (figs. 5 and 6). This is in accord-with Schultz ('37) who found a simi-ex difference in all races examined indeed, in almost all the primates he ed. Schultz was quite impressed by act that the Australian possessed the lowest claviculo-humeral index of all the races studied. As he admits, his series was small (only 7 cases and of unknown sex) and his index was 43 in comparison with other races which varied between 46 and 49. In the present series the index found is even lower, so that the Australian (from the South Eastern part of the continent at least), must be regarded as having a very low claviculo-humeral index,

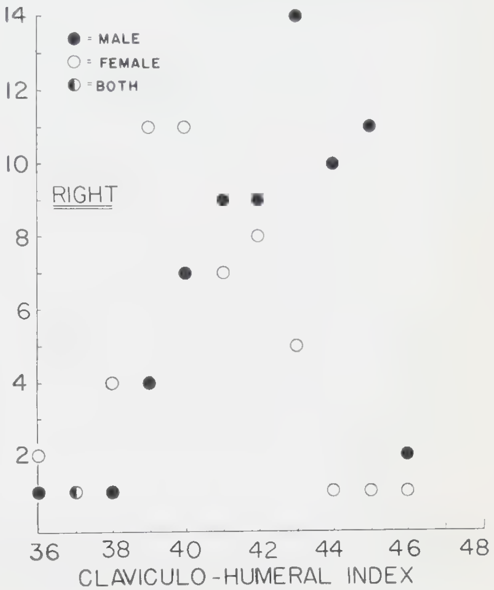


Fig. 5 Frequency distribution of the claviculo-humeral index (right side).

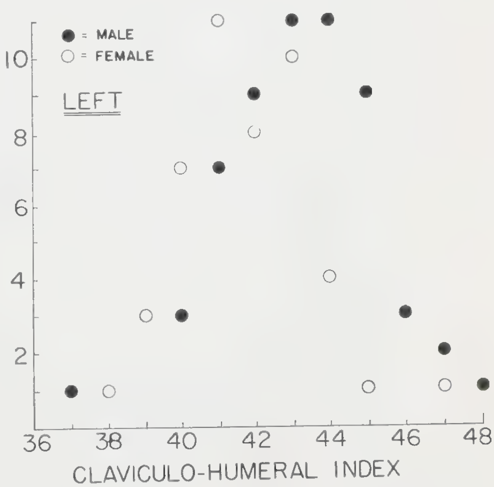


Fig. 6 Frequency distribution of the claviculo-humeral index (left side).

this being of the same order of magnitude as Schultz found for the chimpanzee.

The thickness index. There was, in both the male and the female, a slightly greater thickness index on the right side and a difference between the sexes of about the same degree. The racial difference showed the Australian to have a slightly greater thickness index than either the White American or the American Negro.

The index of the outer end. Again there was in both male and female, a slightly higher index for the right side than for the left although this difference was small. Similarly the difference between the sexes showed the male to have the higher index but by only a very small margin. Racially the results show very little difference.

The index of the inner end. There was very little difference between right and left sides in both the male and the female but a definite difference in favor of the male, between the sexes. Racially the Australian has a lower index than in the English clavicle.

Non-metrical features

In addition to the metrical assessment of the clavicle, an attempt was made to analyze the range of variations of the non-metrical features. It is, of course, obvious that such an assessment is a purely subjective one, but as best as possible, various criteria were applied to each of the non-metrical features studied, and every attempt was made to keep to these standards.

The type of the clavicle. Some clavicles are long and slender, while others are short, thick and generally robust. This difference was a striking non-metrical feature. In between these two extremes, there are, of course, many which are not outstanding, but it was felt that an arbitrary division of the bones observed into the two categories was justified, even though its significance may well be doubtful. In the male 96 clavicles (60%) were classified as long and slender, while 65 (40%) were grouped as short and robust. The corresponding figures for the female were 68 (56%) and 54 (44%) respectively.

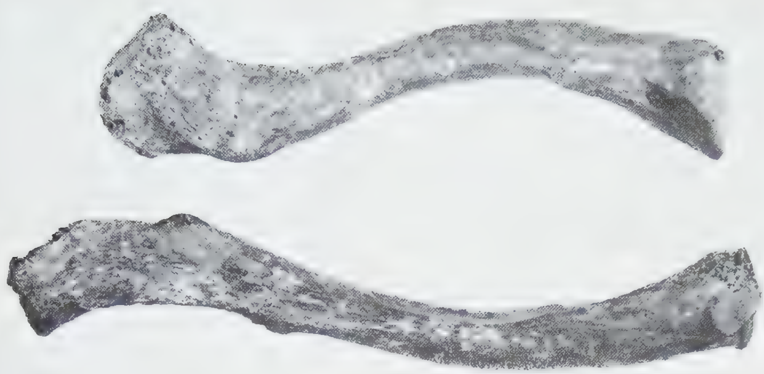
The nutrient foramen. This pres[illegible] a rather difficult problem, for, alth[illegible] the standard texts in anatomy state [illegible] "a nutrient foramen is found in the la[illegible] end of the (sub-clavian) groove . [illegible] (Gray, '44) this was by no means al[illegible] the case. A single nutrient foramen [illegible] not the rule, and its position by no m[illegible] constant. In this study, an attempt [illegible] made to indicate not only the numb[illegible] the nutrient foramina, but also their [illegible] The foramina were, therefore, gro[illegible] into large, medium and small, and [illegible] number indicated by corresponding [illegible] bols. In a few cases there was no de[illegible] nutrient foramen but merely a serie[illegible] small apertures indicating that the [illegible] trient artery entered the bone as a sh[illegible] of small branches.

	1	2	3	4	Mu[illegible]
	Male				
Number	70	69	14	3	[illegible]
Percentage	43	43	9	2	[illegible]
	Female				
Number	45	62	10	0	[illegible]
Percentage	37	51	8	0	[illegible]

When the nutrient foramen was singl[illegible] size was indicated according to the fol[illegible] ing table.

	Large	Medium	Sm[illegible]
	Male		
Number	43	22	[illegible]
Percentage	61	32	[illegible]
	Female		
Number	19	21	[illegible]
Percentage	42	47	1[illegible]

Perforations. Situated as it is i[illegible] superficial position in the body, the c[illegible] icle is crossed by various structures suc[illegible] the supraclavicular nerves and the c[illegible] munication between the cephalic and [illegible] ternal jugular veins. Perforations [illegible] stated to exist with relative frequenc[illegible] the clavicle, but in the present series [illegible] 6 cases were observed of which 5 occu[illegible] in the male and one in the female. [illegible] position of the perforations in all the ab[illegible] cases was on the postero-superior edg[illegible] the bone at about its mid-point or in[illegible]



7 Two male clavicles. The difference in form is particularly evident in the lateral third.

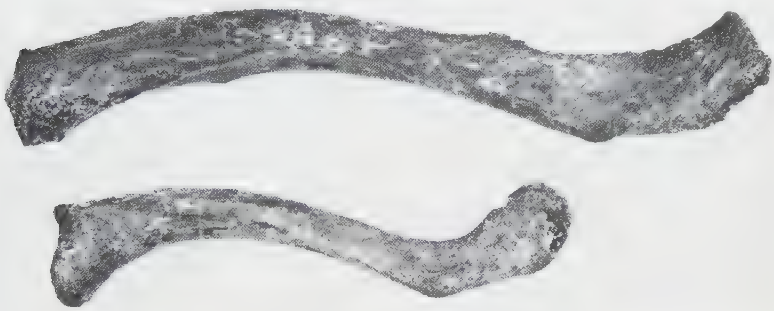


Fig. 8 The longest and shortest male clavicles.

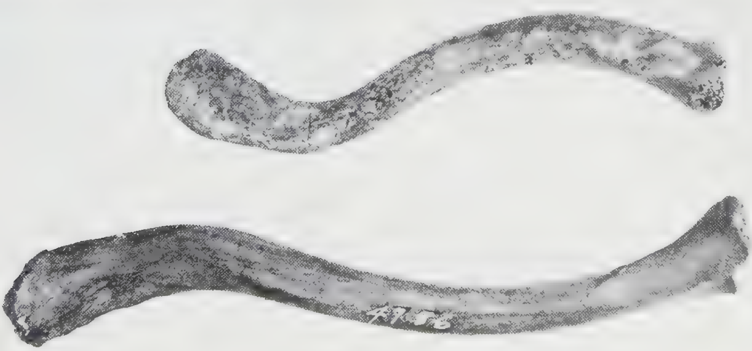


Fig. 9 The longest and shortest female clavicles.

lateral third. The perforations always extended from above downwards and were probably vascular in origin.

The shape of the inner end. The statement in standard texts that "the sternal surface is quadrangular, sometimes triangular, in form" (Gray) is an over simplification but is undoubtedly adequate for normal teaching purposes. In the present study, however, this triangular or quadrangular form was far from satisfactory. The attempt was made to group the shape of the sternal surface of the clavicles into 4 groups, namely, round, oval, reniform and irregular, but it must be pointed out that this classification is purely arbitrary and should not be over-analyzed. Accepting the necessity for such an attempt, however, the results may be summarized as follows:

	Round	Oval	Reniform	Irregular
Male	20 (12%)	31 (19%)	54 (34%)	56 (35%)
Female	18 (15%)	40 (33%)	34 (28%)	30 (24%)

Impression for first rib. The extent to which the first costal cartilage enters into the formation of the sterno-clavicular joint is a variable feature. The range of variation in the development of this facet was substantial. Again purely arbitrary criteria were adopted in defining the size of this facet which was recorded as absent, small, medium and large. The results are as follows:

	Absent	Small	Medium	Large
Male	74 (46%)	47 (29%)	31 (19%)	9 (6%)
Female	68 (56%)	34 (28%)	14 (11%)	6 (5%)

Rhomboid impression. The essential role of the rhomboid (costo-clavicular) ligament in maintaining the stability of the sterno-clavicular joint is well recognized, and it may well be expected that the size of the rhomboid impression on the under surface of the clavicle would be marked in the male, and perhaps not so well marked in the female. The extent and shape of this impression was naturally variable, and the depth was also liable to considerable variation. In many b[illegible] the area for the attachment of this [illegible]ment was shown by a roughening o[illegible] bone, often more readily perceive[illegible] touch than by sight. In other cases [illegible] was a definite impression and in [illegible] again this area was characterized b[illegible] formation of a well-defined pit. A[illegible]ment under such circumstances of th[illegible]tual strength of the ligament is natu[illegible] fraught with considerable difficulty [illegible] it may well be indicated if the actual [illegible] of attachment is considered, rather [illegible] the depth of the pit, if present. This r[illegible]boid impression was, therefore, ass[illegible] in area as absent, small, medium or l[illegible] and the results are shown:

	Absent	Small	Medium	L[illegible]
Male	nil	10 (6%)	40 (25%)	[illegible]
Female	4 (3%)	29 (24%)	60 (49%)	[illegible]

Impression for sterno-mastoid. The [illegible]pression left on the clavicle by the st[illegible]mastoid muscle was extensive and ob[illegible] in some cases, faint and even lackin[illegible] others.

	Absent	Small	Medium	L[illegible]
Male	18 (11%)	62 (39%)	47 (29%)	[illegible]
Female	36 (29%)	48 (39%)	25 (21%)	[illegible]

Impression for pectoralis major. [illegible] clavicular head of the pectoralis m[illegible] muscle constantly leaves a well-define[illegible] pression on the anterior surface of [illegible] medial half to two-thirds of the clav[illegible] In this attempt to assess the degree of [illegible] osseous marking, the impressions [illegible] grouped as

	Absent	Small	Medium	L[illegible]
Male	nil	2 (1%)	41 (26%)	1[illegible] (7[illegible]
Female	nil	45 (37%)	57 (47%)	(1[illegible]

Impression for deltoid. The exten[illegible] the deltoid impression is usually cons[illegible] in a linear fashion, but the degree [illegible] roughening on the bone and the ove[illegible]

› the superior surface are subject to a siderable degree of variation. The an-is of this roughening and overlap was, efore, attempted in a subjective fash- and graded as absent, small, medium arge.

	Absent	Small	Medium	Large
e	nil	29 (18%)	85 (53%)	47 (29%)
ale	1	63 (52%)	52 (42%)	6 (5%)

ubclavian groove. In a well-marked ricle the subclavian groove is sharply ned and is an obvious structure on the rior surface of the bone. It appears ards the medial end, gradually deepens becomes well formed medial to the oid tubercle, at which level it may minate, or else pass for a short distance ral and anterior to it. Even in cases ere the subclavian groove is not read- visible, it is usually palpable, but in ne male and female specimens it could ther be seen nor felt.

	Absent	Small	Medium	Large
e	3 (2%)	28 (17%)	61 (38%)	69 (43%)
ale	12 (10%)	51 (42%)	37 (30%)	22 (18%)

Conoid tubercle. The conoid tubercle sented the classical forms of "a promi- it tubercle" in most specimens but in ne there was no tubercle to mark the of attachment of the conoid ligament. one pair of clavicles the conoid tubercle owed characteristics indicating that it l been developed in association with a responding marking on the coracoid cess of the scapula, thus taking part in formation of a coraco-clavicular joint. is arrangement has been described in ail elsewhere (Ray, '59).

	Absent	Small	Medium	Large
le	1 (1%)	40 (25%)	72 (44%)	48 (30%)
nale	nil	45 (37%)	55 (45%)	22 (18%)

Impression for trapezoid ligament. The eat variability in the shape of the marking for the trapezoid ligament, which ranged from linear to ovoid was a characteristic feature. An attempt was made, by visual means only, to assess the size of the marking with the following results.

	Absent	Small	Medium	Large
Male	nil	54 (33%)	82 (51%)	25 (16%)
Female	nil	76 (62%)	43 (35%)	3 (3%)

Additional facets. No additional articular facets were observed.

SUMMARY

The clavicle of the Australian Aboriginal is definitely shorter in both sexes than in those other races for which figures are available. This fact alone would not be of interest as it might well be a reflection of the general size of the individuals. However, when we consider the other measurements of the clavicle, it can be seen that the circumference of the bone at its mid-point, while less in the Australian is not reduced to the same degree as is the length, so that the thickness index is actually greater in the Australian than in other races. If we consider the minimum width of the bone it is apparent that the Australian exceeds the English in the male and there is little difference in the female. Most other measurements, however, show that the Australian clavicle is smaller than in other races.

Perhaps the most interesting feature is the claviculo-humeral index, which, showing as it does that the figures for the Australian are very low, indicates that the size of the clavicle proportional to the humerus is reduced.

The non-metrical features indicate that, in general, Australian aboriginal bones are well marked by attachments, particularly in the male as in all cases the extent of muscular and ligamentous markings are greater in that sex.

ACKNOWLEDGMENTS

The author is indebted to Mr. Murray Black of South Gippsland in the state of

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Male Reproductive Organs in Certain Gibbons ylobatidae)

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e morphology of the reproductive or- in the various species of gibbons (Hy- idae) is not adequately known. For species virtually nothing is recorded, the remainder are known from data elatively few individuals. Wislocki remarked on the fragmentary na- of current accounts of the external alia of gibbons. Moreover, the data ate considerable variation, at least as ds the external genitalia, the varia- possibly being due to age. Matthews stresses the undesirability of gener- ions based on limited numbers, and ed his data on three individuals for arative purposes when further ma- became available. A review of pres- nowledge on the external organs is by Hill ('58).

e purpose of the present communica- is to present data on the external and nal male organs of a series of gibbons sentative of three recognized groups n the family, with particular refer- to the forms not hitherto, or but ily, referred to in the previous litera- We have therefore concerned our- s particularly with the siamang (*Sym- ingus syndactylus*), the hoolock (*Hy- es hoolock*) and the concolor gibbon *obates* [*Nomascus*] *concolor*). As the us forms of *H. lar* and its near rela- *H. moloch* and *H. agilis* (by some re- ed merely as races of *lar*) are more uently referred to in the literature, are hereafter merely mentioned in ng.

MATERIAL

e following material has been ex- ied:

A. Siamang (*Symphalangus syndactylus* (Desmarest))
   - K.1 Juvenile, total length (vertex-ischium) 285 mm.
   - PA 30 Immature, total length (vertex-ischium) 346 mm.
   - 357/54 Subadult, total length (vertex-ischium) 380 mm, weight 1785 gm.

B. Hoolock (*Hylobates hoolock* (Harlan))
   - K.2 Juvenile, total length (vertex-ischium) 300 mm.
   - PA 26 Subadult, total length (vertex-ischium) 365 mm, weight 2350 gm.

C. Concolor gibbon (*Hylobates* [*Nomascus*] *concolor leucogenys* (Ogilby))
   - PE 80 Newborn, total length (vertex-ischium) 180 mm, weight 394 gm.
   - 286/55 Adult, total length (vertex-ischium) 433 mm, weight 3429.2 gm. (7 yrs, 10 mos. old)

In most cases the external organs have been measured and examined upon the freshly dead cadaver, and the data subsequently confirmed and supplemented after embalming. The internal organs have been studied after embalming and subsequent removal and immersion in a bath of 10% formalin or, in certain cases, after removal of the organs from the fresh body and subsequent formalin fixation.

Histological preparations were made from sections cut at 10 μ thickness and stained in hematoxylin and eosin.

External genital organs

Symphalangus syndactylus

Genital hair. In contrast to the hoolock, the hair of the genital region is less densely planted, permitting the penis to remain

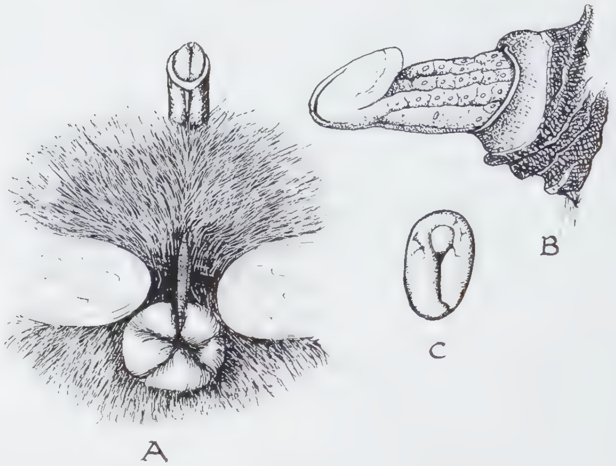


Fig. 1 *Symphalangus syndactylus* ♂ 357/54. External genitalia. A, General view fr the perineal aspect. B, Left lateral view of penis, enlarged. C, Apical view of glans pe

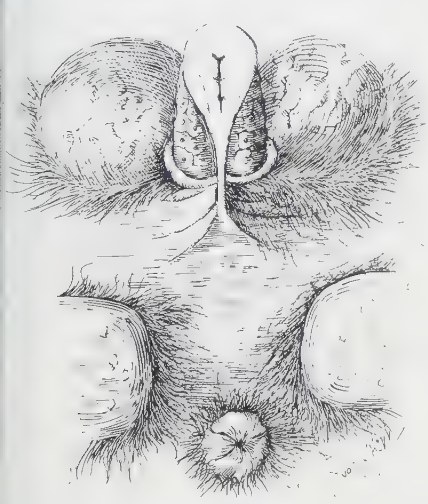
visible although the scrotal area is partially obscured. The genital tuft is not contrastingly colored, but completely black as on adjacent regions. It is longest over the scrotal area, attaining a maximum length of 5 cm. The genital tuft is sharply defined dorsally, ceasing abruptly on the perineal body. Laterally it merges with the hair on perineum and thighs. Over the body of the penis the hair is shorter and distally ceases abruptly some 2 mm proximad of the free margin of the prepuce. Circumanal hairs and those immediately lateral to the perineal raphé are extremely short and very sparsely planted, rendering the parts virtually naked on superficial inspection. No particular direction can be assigned to the hairs in the grown animal, all of them standing out at right angles to the skin surface. The skin itself is not particularly heavily pigmented, even on the naked area of the anal hillock, while the median raphé connecting the scrotal area with the anal opening, traversing the anal hillock in its course, is quite pallid.

Scrotal area. There is no distinct scrotal sac in any of the specimens examined, but merely a prominent area of wrinkled skin some 22 mm across, situated partly parapenially and partly postpenially, with the testes located in the parapenial portion of the structure. There is no indication of bilateral division by a median sulcus; but in the largest animal there is a distinct U-shaped depression betwe base of the penis and the scrotal ski another more peripherally, so that shaped fold of scrotum encircles t nial root laterally and around the pe side. This is not so clearly indica PA 30, where the scrotal area is som paler and less rugose. A median crosses the angle between the root penis and the scrotal area, dividi U-shaped groove at its apex. The is eventually continued, as already tioned, to the anal margin, crossi ventral part of the anal hillock to the margin of the orifice (fig. 1.)

Penis. The general form of the closely recalls that of *Hylobates ag* described and depicted by Matthews

The organ projects forward fro symphysis in a well-developed pigm prepuce which, however, fails to cov glans. The free margin of the pr extends to the junction of the middl distal thirds of the pars libera, the third and glans remaining naked. glans is fairly deeply pigmented, bu collum penis and pars intrapreputia the pars libera less markedly so. The shows less lateral compression than *hoolock*, but this is noticeable in 35 though not in K.1 or PA 30. The c (or exposed part of the corpus adj to the glans, which is constricted pared with the rest of the corpus) is the glans, covered with an epith

ch presents transverse rows of minute
ıtinized spicules, smaller than those in
ıoolock.
he button-like glans is sharply demar-
:d from the collum on dorsum and
s by a well-marked corona, but the
:-coronal sulcus slopes obliquely down-
ds and distad from the dorsum, the
ına becoming less distinct towards
perineal aspect of the penis. This ar-
gement is much as in other gibbons,
ng the organ an appearance reminis-
t of its female homologue. The apical
tour of the glans, however, is more
vex than in the typical gibbons of the
us *Hylobates*, its true apex being slight-
ıearer the dorsum and above the ure-
ıl slit. Beneath the prominence of the
x is a Y-shaped groove, the stem of
ıch is bounded by the lips of the urinary
ıtus. The stem of the Y incises the in-
or margin of the glans adding still
her to the clitoris-like appearance and
ıarting a lobate character to the in-
or extremity of the meatal lips.
he frenulum praeputii is a very short,
ı fold commencing well proximal to
corona glandis, but connected there-
ı by an exceedingly faint ridge which
omes apparent only when the prepuce
ully retracted.
rectile tissues and baculum. The site
ıttachment of the root of the penis to



ig. 2 *Hylobates hoolock* ♂ PA.26. External
italia; general view from the perineal aspect.
e prepenial site of scrotal swellings.

the pelvis is of some significance in estimating the systematic position of the gibbons. The question is considered below under "Discussion," but for the moment the facts regarding *Symphalangus* may be stated.

The pars libera of the penis in *Symphalangus* leaves the parietes at the caudal end of the symphysis pubis; the distance from its dorsum to the cranial edge of the symphysis being 21.5 mm. This contrasts with the normal arrangement in catarrhine monkeys, where the corpus penis travels forwards along the ventral aspect of the symphysis before becoming "free" at its cranial edge.

The crura penis are relatively shorter, and more flattened cranio-caudally, than in *Hylobates hoolock*. They present a fusiform outline and extend over the proximal 14.5 mm of the penial root. The bulb of the corpus spongiosum is relatively poorly developed.

The baculum is small, rod-like, but narrowing gradually to its tip, and surrounded by dense periosteum derived from the corpus fibrosum. Gerhardt ('10) recorded a baculum 14.5 mm long with proximal end 2.5 mm thick in a presumed adult siamang. He noted a much smaller structure in a younger specimen.

Hylobates hoolock

Genital hair. Hair surrounding the genitalia is of a darker hue than on the adjacent part of the thighs, being jet-black without any brownish wash. The pelage here forms a distinct genital tuft similar to that in the female (Pocock, '27; Matthews, '46; Kanagasuntheram, '54) being somewhat longer than on adjacent areas. The longest hairs measure 25 mm.

On each side of the base of the penis the hairs are densely planted, completely hiding the scrotal area. They are more sparsely planted above the dorsum of the penis, so that the distal part of the corpus penis and the entire glans are visible without disturbance of the pelage (cf. Goss, '47, *Gorilla;* Hill and Matthews, '49). Nevertheless, it is difficult to determine the sex from external inspection of the living animal short of manual assistance, for the grooved glans penis bears, as in *Symphalangus*, a striking resemblance to

a hypertrophied clitoris. On either side of the penis, particularly towards the anal hillock, the dark genital tuft is interspersed with a few lighter hairs ranging from dark brown to gray. Hair tracts are continued around the periphery of the naked callosities and at their lateral extremities the hair is of slightly lighter hue. The hair immediately around the root of the penis is also lighter and shorter in some individuals.

Hairs of the genital tuft contrast with the general body pelage in being relatively straighter and less woolly in texture. The woolly body hairs when artificially extended exceed the genital hairs in length. Hairs on the penial skin are much shorter, and decrease in length distally. They are also much finer than those of the genital tuft. Hairs cease abruptly some 3 mm proximal to the free edge of the prepuce. All the penial hairs present a distad trend.

On the perineum the hairs point medially as in *Gorilla*, but those ventral to the anal hillock are directed towards the scrotal area.

Scrotal area. Ovoid swellings 20 mm sagittally and 12 mm in transverse diameter are located prepenially with their caudal ends level with the root of the penis. These are produced by the subcutaneously placed testes. The overlying skin is not specially modified. This anterior portion of the scrotal area is demarcated by a transverse groove from a postpenial area which is homologous with the true scrotal sacs of most eutherian mammals. This hinder region of the scrotal area is quite empty. It is traversed in the median line by the peno-scrotal raphé which is continuous anteriorly with a penial raphé and dorsally with the perineal raphé, which terminates at the anal margin. The skin over the postpenial scrotal area is more wrinkled than that over the testes, which is quite smooth. Both areas are fully haired and obscured.

Penis. Relatively small in proportion, the pars libera projects forth from the surface of the body at a level some 25 mm caudal to the cranial edge of the symphysis pubis. The organ is covered by a pigmented cutaneous prepuce over its proximal 9 mm, the remainder, which includes part of the body and the whole of the glans being uncovered. The unclothed part as heavily pigmented as the prepuce. exposed part of the collum and co and the intra-preputial part of the libera are bedecked with horny spic These are implanted with their b (some 0.5 mm diameter) forming a saic pattern in the surface epithel Their apices form nodular or sli longitudinally-ridged elevations witho with but very slight proximad trend some of the nodules these apices marked by concentrations of pigmen others the bases are encircled by pigr concentrations. Intervening epitheliu not evenly pigmented when viewed m scopically, the granules being deposite wavy lines resembling watermarks paper or silk.

In the fresh state the collum and posed corpus are marked by a median sal sulcus.

The glans is compressed transve and of approximately conical form. strongly demarcated from the collum a corona and retrocoronal sulcus. T is a strong lateral concavity on the p mal border of the corona, but the prox extent is approximately equal on the sum and perineal aspects, though the ferior lappet is narrower transversely t the broad dorsal flange. From the edg the inferior lappet a median elevatio keel continues proximad to becom raphé on the prepuce, and thencefort the peno-scrotal raphé as already m tioned.

The distal surface of the glans is mar by a deep median groove extending the dorsum, from a point mid-way betw the corona and the apex, continuing the apex and on to the inferior surfac far as the corona. The urinary meatus in the depths of the inferior half of groove, thus contrasting with its site for example, *Macaca sinica* where it in the dorsal part of the groove.

Erectile tissues and baculum. The b of the penis emerges from the body at approximately the same position a *Symphalangus*. Proximal to this the th components of the radix penis resem those of *H. concolor* described below, the crura appear to be more cylindrica

hough not demonstrated radiographic- (cf. Hill and Matthews, '49, pl. IV, F), there is a well-ossified baculum in specimens we have studied micro- ically. In K.2 the baculum is 3 mm . Microscopically the bone shows ctural similarities with a typical long e, having a central medullary cavity taining bone-marrow, surrounded by npacta exhibiting typical Haversian ems. Peripheral to this is a region of ification in which Haversian systems e not yet made their appearance. Ex- ıal to this zone, the connective tissue undergone a hyaline change with the tained corpuscles taking on the char- er of osteoblasts. Under high power pecially with oil immersion) the proc- s of the osteocytes can readily be seen ning a network of interlacing strands . 11). The presence of Haversian sys- is in the baculum contradicts the ac- ted view that these develop only where re is great tensile stress.

obates concolor

Genital hair. In the fetus this is en- ly lacking, the whole genital area being le except for a very fine coat of white, y lanugo hairs covering the scrotum, ble only on high magnification. These rs are close-fitting and exhibit a con- gent trend towards the median raphé the direction of the fundus of the sac. the raphé itself they are directed sagit- y. No similar hairs occur on the penis, puce, pubic region or perineum.

n the adult the whole genital region clothed in a dense tuft of black hairs ich completely obscure the genitalia. the scrotal area these attain a length over 15 mm. They are shorter around root of the penis and on the perineum d therefore present an exaggerated pic- ture of the state in the fetus with the added feature of deep pigmentation.

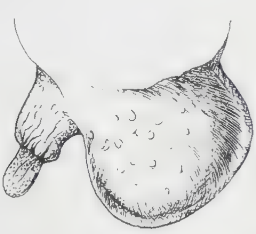


Fig. 3 *Hylobates concolor leucogenys* ♂ new- n, PE.80. Left lateral view of external geni- ia.

Scrotal area. In both fetus and adult there is a definite scrotal sac. It is particularly well defined in the fetus, where it constitutes a pear-shaped dependent integumental bag without external indication of its paired character beyond the presence of a well-defined raised median keel-like raphé which extends from the peno-scrotal angle to the perineo-scrotal angle. On the posterior wall of the scrotum the raphé becomes more accentuated and at the perineo-scrotal angle it presents a triangular surface each side (see fig. 3). Dorsally the raphé is continued as a feebler fold over the short (9 mm) perineum to the anal margin. Ventrally it is continued as the median raphé of the prepuce.

Dimensions of the sac are given in table 1; it may be added that in the fetus the transverse diameter at the neck is 10 mm, the height of the sac from the femoro-scrotal groove to the fundus 11.0 mm, and its dorso-ventral diameter 20 mm. The adult scrotum is more globular and sessile, its antero-posterior and transverse diameters being approximately equal, but the dorso-ventral dimension only half as much. The scrotal integument is darkly pigmented. Dorsally, the scrotal wall impinges on the ventral margins of the callosities which just meet in the mid-line where their junction affects the whole depth of the short perineum from perineo-scrotal angle to the ventral edge of the anal hillock. The distance from peno-scrotal angle to center of anus is 25 mm.

Penis. In the fetus the pars libera is clothed by a thick but short prepuce which is unpigmented and virtually hairless, but the laterally compressed glans projects freely and contrasts in its deep pigmentation, this being the only obviously pigmented structure on the body surface at this stage. The prepuce is finely wrinkled and towards its free end narrows abruptly, the rolled free margin being crenulated. The corpus and glans are not sharply demarcated, the whole structure taking the form of a laterally compressed cylinder with smoothly rounded distal profile. A few faint longitudinal grooves mark its side, but no spicules are yet developed. The elongated meatal slit is directed in-

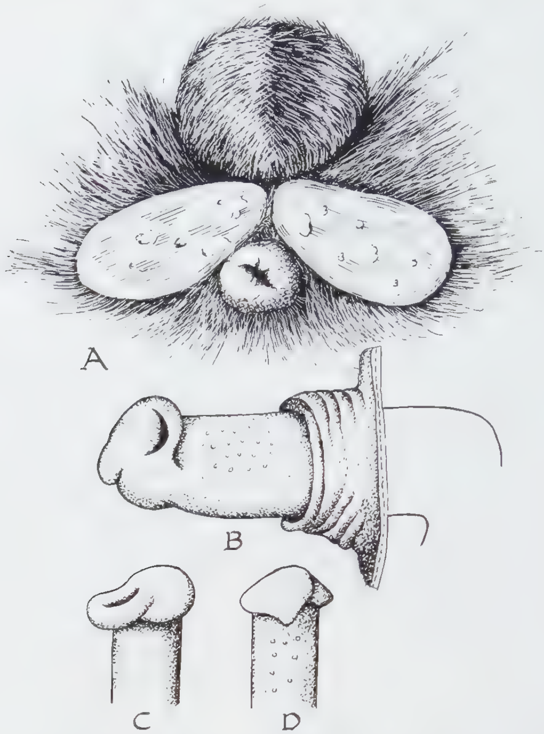


Fig. 4 *Hylobates concolor leucogenys* ♂ adult, 286/55. External genitalia. A, General view from the perineal aspect (penis entirely hidden by hairy scrotum). B, Left lateral aspect of penis, enlarged. C, Dorsal aspect of pars libera of penis. D, Ventral aspect of same.

TABLE 1

Measurements of the external genitalia

	Siamang			Hoolock		Concolor	
	357/54	K.1	PA 30	K.2	PA 26	PE 80	28[illegible]
	mm	*mm*	*mm*	*mm*	*mm*	*mm*	[illegible]
Length of pars libera	18	17	18	15	17.2	11.4	[illegible]
Tr. diameter of pars libera (at root)	6.6	7	7.5	7.5	7.2	5.6	[illegible]
Tr. diameter of collum penis	3.7	4	3.5	3.5	3.2	1	[illegible]
Proximo-distal length of glans	4	3	3.5	4	3	3.7	[illegible]
Trans. diameter of glans	4	4.5	5.5	4	3.8	1	[illegible]
Sagittal diameter of glans	7	—	5.6	—	5.3	2.5	[illegible]
L. of pars intrapreputialis corpus penis	8.2	2.5	6.5	2	4.7	1.5	[illegible]
L. of meatus urinarius externus	3	2.5	3.5	4	2	3	[illegible]
Trans. diameter scrotal area	22	—	21	—	23.5	13.5	[illegible]
Sagittal diameter scrotal area	16		17.8		26.3	17.4	[illegible]
Baculum length	3.5	2.5	—	3	—	—	[illegible]

rly on the distal part of the glans. organ thus recalls that of the adult g-utan.

ne adult penis differs considerably that of the newborn. The distinc- are (1) the increased pigmentation h now affects all parts of the external alia, i.e., prepuce as well as glans scrotum, (2) the marked delimitation ans from body by the growth of a cor- glandis, (3) the alteration in shape of glans, which has approached that of other adult gibbons herein described, (4) the development of keratinized ıles on the pars intrapreputialis.

s regards finer details, it is difficult to bsolutely dogmatic from the material lable. The only adult male available not examined in the fresh state and subjoined remarks are therefore based xamination of the embalmed cadaver further detailed study after removal of parts. The glans shows such marked nmetry that it may be argued that -fixational distortion has occurred; on the other hand it must be stated the glans was almost entirely en- ıthed by the prepuce and was thereby ected. Further protection was pro- d by the hairs of the dense genital . The details affected can be best un- stood by inspection of the accompany- figures. It will be noted that there is vell-marked corona glandis, except in- orly on the left, where the distal sur- e of the glans passes almost impercept- on to the collum. Immediately above , however, the corona is better devel- d than elsewhere, forming a lobate minence projecting proximad over the um. This lobate appearance is en- ıced by virtue of a slight groove con- ıed from the corona on to the upper t of the distal surface of the glans ır the presumed median line. To the ht the corona is more normal. On the ineal aspect the corona provides a slight dge-shaped proximal extension in the dian line. The urinary meatus is a scentic slit with its concave supero- eral lip lying parallel with the margin the lobate portion of the corona some mm distant therefrom.

On the sides of the pars intrapreputialis reticular pattern is produced by the bases of the keratinized spicules whose sharp apices are directed proximally. A few scattered more papilliform spicules adorn the perineal aspect of the corpus. They are lacking from the glans and from the dorsum of the penis.

Erectile tissue and baculum. In the adult the body of the penis leaves the pubic region some 18 mm posterior to the anterior edge of the symphysis. Here the erectile cylinder undergoes a sharp bend some 16 mm proximal to the free tip of the penis. Less than half the length of the corpus penis therefore is pars libera, the remaining 28 mm being buried in the tissues of the body wall.

The baculum was not demonstrated in the fetus. In the adult it is better developed than in any of the other gibbons examined. It attains a length of 9 mm, i.e., thrice the length of the average of the other specimens. It also differs in shape, being dorso-ventrally compressed (1.0 mm thick) but transversely expanded (2.5 mm) at its base, yet narrowing uniformly distally. It therefore presents in dorsal view the outline of an isosceles triangle.

Internal genital organs

The three species may be conveniently considered together and their differences compared in passing, since these are less than in the external organs.

Testes. Measurements are given in table 2; and their location has already been considered in dealing with the scrotum.

Each gland may be described as ovoid, with cranial and caudal poles and three principal surfaces, antero-medial, antero-lateral and posterior, separated by three borders, anterior, postero-lateral and postero-medial. The epididymis is applied to the lateral side of the back of the testis.

In the adult *H. concolor*, which is sexually the most mature of the whole series, there is a distinct narrowing of the cranial pole of the testis, whereas the caudal pole is distinctly more rounded. The ductus deferens lies along the posterior border, with the sinus of the epididymis directed anteriorly and laterally in all three species. The body of the epididymis lies dorsal to the ductus along the postero-lateral surface of the testis. The cauda epididymis is broadly adherent to the tunica vaginalis

TABLE 2

Measurements of the internal genitalia

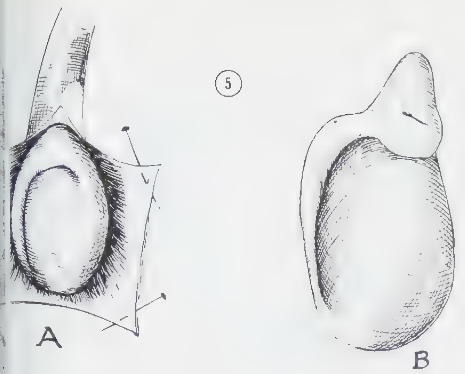
	Siamang			Hoolock	
	357/54	K.1	PA 30	K.2	PA 26
	mm	*mm*	*mm*	*mm*	*mm*
Testis					
Length	10.2	9.0	12.7	9.0	9.8
Trans. diameter	5.2	3.5	3.7	3.5	5.8
Dorso.-vent. diam.	7.0	6.0	8.5	5.0	7.8
Spermatic cord					
Length to apex of ext. abd. ring	24		15.8		24.5
Diam. max. (near testis)	6.8		6.9		6.3
Diam. min.			4.7		4.9
Ductus deferens					
Length	123.5	100			
Ext. abdominal ring					
Medial pillar	10.5		12		9.0
Lateral pillar	9.8		8.8		10.5
Base	3.0		7.0		5.0
Between right and left ring	—		7.6		8.8
Urethra					
Prostatic portion, l.	13.5	10	10	9.5	9.0
Membranous portion, l.	5.5	4	5.5	3.5	4.5
Penile portion, l.	32.5	19	24	18.5	18.5
Vesicula seminalis l.	11.2	15	6.1	5	—

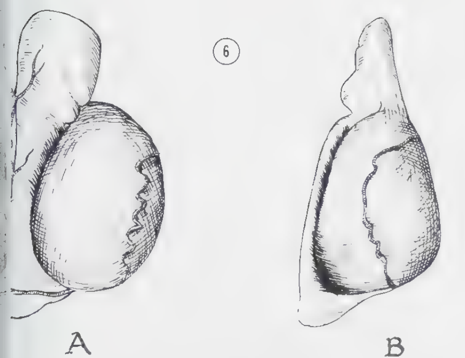
at the fundus of the scrotal sac, especially in *Symphalangus* and *H. concolor.* The caput epididymis is of compressed pyramidal form and projects into the proximal extension of the tunica vaginalis. In the adult *H. concolor* it resembles a cocked hat, rising an additional 10 mm above the cranial pole of the testis. It is laterally compressed, and its ventral border presents, near the cranial pole of the testis, some minor crenations, one of which serves as a vascular hilum since a branch of the spermatic artery enters the caput here. A thick fold of tunica vaginalis connects the ventro-medial part of the caput with the cranial pole of the testis.

In the epididymis of the hoolock, the epithelium is of the simple cuboidal type, without cilia: the lumen contains a colloid-like substance. In the siamang, the epithelium tends to be stratified columnar, with cilia.

In the hoolock (K.2), which is about two years old (corresponding to an 8-year-old human), the seminiferous tubules do not show active signs of spermatogenesis. There are 2–3 strata of cells between basement membrane and the lumen the tubule. Relatively more layers of are found in a 4-year-old child, but characteristic feature of the seminife tubule in *Hylobates* is the presence number of very large cells with eos philic cytoplasm. These are not unifor distributed throughout the tubules; so tubules possess several, others have no When present, these cells tend to lie n the basement membrane, while a few cur closer to or even inside the lum Some of these cells are multinucleat in such instances they are found to closer to the lumen. The multinuclea cells show two or three nuclei without totic spindle. The human testis prese nothing homologous to these multinu ated cells. In the hoolock they are proba primordial sex cells. They are present, less evident, in the siamang.

Tuncia vaginalis and spermatic co Testis and spermatic cord are provic with the usual coverings, i.e., extern cremasteric, and internal spermatic f





5 *Symphalangus syndactylus* ♂ 357/54. testis. A, Lateral view with envelopes. ıe same removed from its envelopes and vhat further enlarged.
6 *Hylobates concolor leucogenys* ♂ 286/ tight testis. A, Lateral view; B, anterior

The cremasteric layer is fleshy, con- g of loops of pale muscular fibers :d apart with intervening areolar tis- These are traceable back to the par- on the dorsal side, as found by Miller in *Hylobates* ? sp. No essential dif- ce was found between the three spe- studied. Cremasteric fibers are de- in part from that portion of the in- l oblique muscle arising from the lat- 'ourth of the inguinal ligament. They einforced by fibers arising from the ıl half of the inguinal ligament.
e cord, of flattened cylindrical form, rm in diameter (6.8 mm) throughout *ymphalangus*, but narrowed at its mal end in *H. concolor* and *H. hoo-* has a length of 18–21 mm between pper pole of the testis and the base of xternal abdominal ring (level of cra- order of symphysis pubis).

The tunica vaginalis is an elongated ovoid sac enclosing the testis and epididymis and extending some 12.5 mm proximad within the spermatic cord, where it usually ends blindly, as in man. In one hoolock (K.2) the saccus vaginalis communicated freely proximally with the peritoneal cavity. A sinus or digital fossa some 5 mm deep, with the serous layer of tunica dipping into it, occurs between the testis and the corpus epididymis, facing laterally.

Inguinal canal. The cord enters the abdominal parietes at the external abdominal ring. This is a deficiency in the external oblique aponeurosis, shaped like a scalene triangle, with its apex directed cranially and somewhat laterally. In the largest *Symphalangus* the lateral pillar is 9.8 mm long, the medial pillar 10.5 mm and the short base 3 mm only. Medial pillars of the two sides are 8.5 mm apart—rather more in *H. concolor*, where the apices are 28.5 mm apart. There are well-developed intercrural fibers, as also recorded by Miller ('47).

Constituents of the cord travel obliquely along the inguinal canal from external to internal abdominal ring. As found by Miller, the internal oblique and transversalis fibers in the caudo-medial part of the abdominal wall are poorly developed on account of their contribution to the cremasteric fascia. Their fibers arch (tendo conjunctivus, falx inguinalis), being inserted on the ventral wall of the rectus sheath well cranial to the pubis. This results in a relatively large internal abdominal ring.

The length of the inguinal canal is 11.6 mm in the larger *Symphalangus*, 11.0 mm in *H. hoolock* (PA 26), and 11.3 mm in the adult *H. concolor*.

Ductus deferens. Sections of the ductus deferens adjacent to the testes exhibit a stratified columnar epithelium without cilia in the hoolock. The muscular coat consists predominantly of circular fibers with a few longitudinal fibers interspersed. In *Symphalangus*, the epithelium is stratified columnar, with cilia. The longitudinal muscle bundles are more distinct than in the hoolock. Macroscopically, in all three species, the ductus exhibits the characteristic whipcordlike texture due to its thick wall and relatively small lumen.

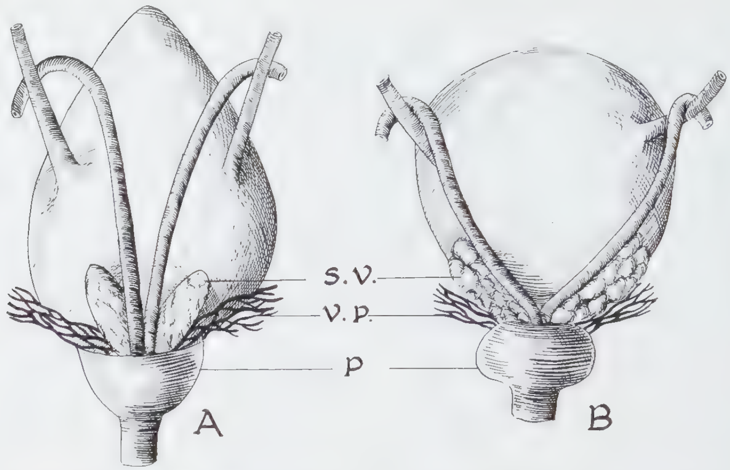


Fig. 7 Internal genital organs and bladder in: A, *Symphalangus*; B, *Hylobates concolo*. P, prostate; S.V., seminal vesicle; V.P., venous plexus.

Vesicula seminalis. This is a short body of fusiform outline with slightly nodular surface; but the lobules are much compacted and the whole surrounded by dense connective tissue, related postero-dorsally to a close-meshed venous plexus. Antero-medially the organ is closely related to the terminal portion of the ductus deferens. Its duct enters the prostate and unites with the ductus deferens to form the ejaculatory duct, which opens into the prostatic urethra.

In size, the vesicles are somewhat variable (see table 2) both in length and width, the variations being doubtless due partly to age and partly to physiological condition. Thus, the smaller *Symphalangus* has vesicles 15 mm long and 2 mm wide; whereas those of the larger animal are only 11.2 mm long and 3.2 mm wide, with their apices 18 mm apart. In the hoolock (K.2), the vesicles were only 5 mm long, but 2 mm broad opposite the middle of the organ, which tapers gradually towards both ends. Histologically, the glands present a close resemblance in structure to that of the ductus deferens. The mucous membrane does not present the intricate system of branching which is characteristic of the human seminal vesicle. However, the single tube is folded on itself so that it is cut 4 or 5 times in a single section. In the siamang, the branching of the mucous membrane is more evident, but the tube is not so markedly f on itself.

The ejaculatory duct (4 mm lon K.2) opens into the urethra, but ex a well-marked dilatation near the ope

Prostate. This is a thick, rounded ramidal structure with the apex di caudad. Its base is apposed to the ne the bladder in *Hylobates;* but in *Sym angus* the bladder forms a narrow proximal to the base of the gland, s the trigone is not in direct appo therewith. In *H. hoolock* (K.2), the has a transverse diameter at its ba 11.0 mm and a sagittal dimension c mm. The bulk of the gland lies dorsa lateral to the prostatic urethra, but a stratum of tissue forms an isthmus the pubic aspect of the urinary pas In *H. hoolock* a shelf of prostatic tissu jects cranially and dorsally around neck of the bladder, lying lateral t common ejaculatory ducts. This take form of paired lappets passing dors the bladder and lateral to the com ejaculatory duct each side. The pro isthmus consists mainly of smooth cle fibers: in *Symphalangus* it con no glandular tissue, but in *H. ho* glandular tissue extends more ven towards the isthmus.

Bulbo-urethral glands. These are s paired, lobulated bodies, some 3 m diameter, lying on either side of the

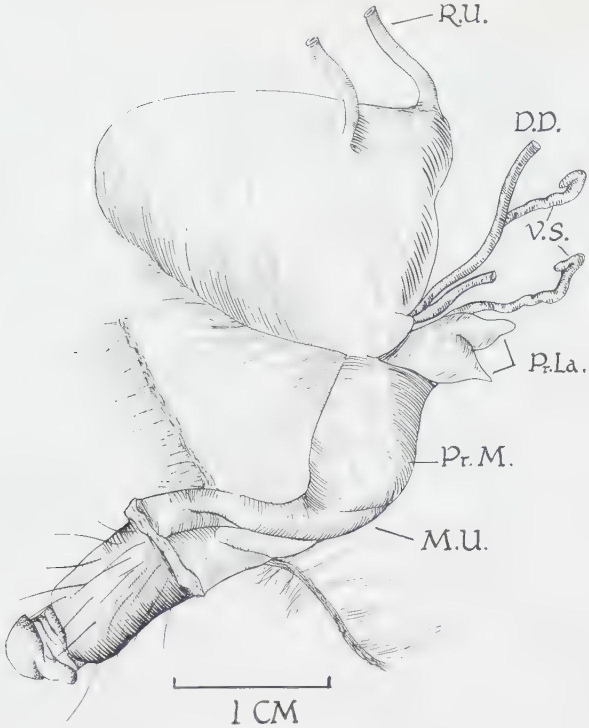


Fig. 8 *Hylobates hoolock* ♂. Dissection of the urogenital tract from the left side. × 2. D.D., Ductus deferens (right); M.U., membranous urethra; Pr.La., lateral lobes of prostate; Pr.M., median lobe of prostate; R.U., right ureter; V.S., vesiculae seminales.

us urethra just proximal to the bulb e urethra. Their ducts run ventrally en into the bulbar part of the penile ra and are about 10 mm long.

thra. This shows the usual subdi- into prostatic, membranous, and portions. Their dimensions are in table 2.

in man, the prostatic urethra is the t section of the tube. Its dorsal wall a globular swelling, the colliculus alis or verumontanum, some 2 mm ameter, sharply defined around its except in the median line, where a ongitudinal fold proceeds distally in ecies, with an additional proximal n *Hylobates concolor* (fig. 8, B). In *halangus* the proximal ridge is lack- ut the distal one is flanked by paired nedian ridges, separated from the n fold by deep sulci (fig. 8, A). The ulus is more circular in circumfer- n *Symphalangus*, but pyriform (with arrow end at the neck of the bladder) *concolor* and *H. hoolock*.

The summit of the colliculus bears, in all specimens of *Symphalangus*, a Y-shaped depression leading to the opening of the utriculus prostaticus, but the openings of the ejaculatory ducts are barely visible to the naked eye. They lie immediately laterad of the prostatic utricle. On the other hand, the openings of the ducts from the prostatic glands are well seen in the groove (sinus prostaticus) to the side of the base of the colliculus. In *H. concolor* the utriculus presents a rounded opening. In *H. hoolock* (K.2) more of the openings were visible to the naked eye, but in PA 26 the utriculus opens by a 1.0 mm long slit on the summit of the 3 mm long oval colliculus. Even under high magnification the ejaculatory ducts could not be distinguished.

The membranous urethra in all three species is relatively elongated, with a thick wall, caused by the amount of striated muscle fibers constituting the compressor urethrae (fig. 9).

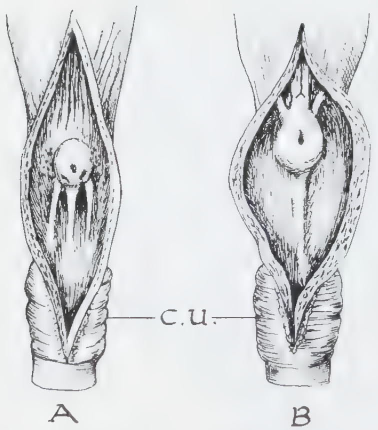


Fig. 9 Interior of prostatic urethra (opened from ventral side) in: A, *Symphalangus;* B, *Hylobates concolor leucogenys.* C.U., compressor urethrae muscle.

The penile urethra is slightly dilated in the bulb, but elsewhere is collapsed, with a stellate lumen in section, except in the glans, where there is a marked dilatation (fossa navicularis) of fusiform outline. Minute blind pockets or urethral lacunae, with distally directed mouths, occur as in the human urethra. The submucosa contains numbers of mucous glands whose ducts penetrate the mucous membrane, except in *Symphalangus.*

In both siamang and hoolock the prostatic urethra is lined by a transitional epithelium of three to 6 layers of cells. Where the lining consists of three layers of cells, those adjacent to the lumen are flattened.

The penile urethra in *H. hoolock* exhibits a lining of transitional epithelium, but in the glans this changes to a stratified squamous epithelium. There are several glandular outgrowth from both penile and glandic portions of the urethra. In the siamang the penile urethra is lined by transitional epithelium, which is without glandular outgrowths.

DISCUSSION

One of the most controversial matters in the genital anatomy of gibbons is the presence or absence of a scrotum or a scrotal anlage. Wislocki ('36), considering the earlier literature, indicated that his own conclusions were at variance with previous statements. As far as gibbons are concerned, Wislocki believed that, as
with catarrhine monkeys, a scrotal a
is developed in fetal life and persist
that permanent descent of the testes
not occur until some time durin
juvenile period. He noted that the m
ity of gibbons were unique among
World primates in the location of the
tum, i.e., bilaterally parapenial or
prepenial rather than postpenial, bu
Symphalangus and *Hylobates concolo*
fered from other gibbons in havi
postpenial scrotum. Sonntag ('24), o
other hand, declared the scrotum
lacking in gibbons, and Pocock ('25
of the same opinion. Welch ('11)
however, described a conspicuous
non-pendulous scrotum in a *H. hai*
(= *H. concolor*), which was attain
maturity during captivity, in contras
H. leuciscus (= *H. moloch*) which
to develop scrotal sacs during the
examined. Welch reached the conc
that scrotal development and test
descent in all gibbons was relative
tarded compared with other Primates
observations were confined to living
mals and museum skins. In *Symph*
gus, Selenka ('03) found a pend
scrotum in the fetus; and Mijsberg
mentions one in an older animal; wh
in fetal specimens of *H. concolor,* th
mer author found the scrotum in tw
apenial halves. Matthews ('46)
small parapenial sacs in a *H. agilis*
reached maturity during captivity;
writer reviewed the earlier literature,
ing that much inconsistency still
(see also Hill, '58).

Summarizing the findings in the
ent series, it is to be noted that in no
the siamangs examined was there a
nite sac, the testes remaining in parap
pouches. Possibly none was old en
to have reverted to the fetal condition
by Selenka and attained in the adu
amined by Mijsberg.

The large pendulous scrotum of the
H. concolor examined by us conforms
that of Selenka's fetal siamang and
fers from that of his fetal *H. concolor.*
existence of a globular, subpendu
densely-haired, postpenial scrotum i
adult *H. concolor* is confirmed.

No previous records relating to *H.*
lock are available. In our materia

tunately subadult, the testes lie subally in a prepenial position. Possibly, advancing age, further scrotal dement may occur in this species.

the whole, our material confirms the hesis of retarded descent of the testes species of gibbons, and supports the that postpenial scrotal sacs appear g fetal life; that the testes are there- withdrawn only to return, if at all, perineal site during late adolescence, ining pre- or parapenial for a matter o 6 years. Only in *H. concolor* does crotum become densely haired.

genital tuft is well developed in *H. lor* and *H. hoolock*, obscuring the exl genitalia and contrastingly colored e latter. In *Symphalangus* the geniairs are lengthened, not contrasted in but more sparsely planted than in *oates.*

e penis is short and inconspicuous in e forms examined. The glans is, in al terms, similar in its truncated and obliquity of its distal surface, as as in its proximal extent on the periaspect of the corpus penis. This fea- together with its small size, gives o a clitoris-like effect, especially with left-like appearance of the meatus rius, continued inferiorly almostly to orona—an appearance which Kohlge (1892) likened to hypospadias. It the similarity between the genitalia e two sexes which led Harlan (1826) scribe the type female specimen of *oncolor* as a "hermaphrodite sia- g." All species agree in the presence orny spicules on the pars intraprelis. *Symphalangus* and *H. hoolock* in the demarcation of polygonal ae around the bases of the spicules. glans is deeply pigmented in all speexamined, even the fetus of *H. con-*, which thus differs from the *H. c. olor* described by Welch, in which the was dull red, contrasting with the ented prepuce.

e attachment of the penis to the peltructures is similar in all. The level hich the pars libera emerges from ody wall is at the hinder edge of the hysis in *Symphalangus* and *H. hoo-* a shade more anteriorly in *H. con-*. These positions align the gibbons with man rather than with the catarrhine monkeys, though *H. concolor* approaches the arrangement seen in *Cebus* as depicted by Mijsberg's figure 6 (p. 17). Mijsberg regards the caudal position of penial emergence as the more primitive, the cranial migration along the ventral surface of the pubis in cynomorphs being a specialization.

The presence of a small os penis in all the species examined confirms previous reports of its existence in the family. It is best developed in *H. concolor*, but is not ossified in the full-term fetus. Yet de Beaux ('17) recorded one 2.7 mm long in a very young specimen. Gerhardt ('10) had reported a small baculum previously in *Symphalangus*, and larger bones in *H. agilis* and *H. leuciscus* (= *H. moloch*). Matthews depicts the bone in *H. agilis* as taking up the major part of the glans dorsal to the urethra.

Little for comment emerges from our observations on the internal organs. Notable are the variable site of the testes—already discussed in dealing with the scrotum—the elongated form of the caput epididymis and the broad adhesion of the cauda epididymis to the fundus of the saccus vaginalis. The variable nature of the epithelial lining of the canal of the epididymis is to be noted, and it is unfortunate that the material was insufficiently well fixed for comparison to be made with the accurate findings of Heidenhain and Werner ('24) on the human epididymis. Possibly the variations we have observed between *Symphalangus* and *Hylobates hoolock* in this feature are to be related to different physiological phases of activity.

Our observations on the cremaster muscle confirm the findings of Miller ('47); but we have not been convinced that Mijsberg's statement that the caudal fibers are derived solely from the transversus abdominis is consistently applicable. Mijsberg maintained that *Hylobates* differed in this respect from *Macaca* and *Semnopithecus*, in which caudal fibers of the cremaster are derived from the obliquus internus.

Peritoneal relations, as Mijsberg found, are exactly as in man, and *Pan*. There is no serosa in the funiculus, no mesoepididymis, while the greater part of the epididy-

mis and the whole of the ductus deferens are retroperitoneal.

Our observations on the seminal vesicles and prostate agree well with those of Mijsberg and Matthews, but we note the difference between *Symphalangus* and *Hylobates* in the relation of the prostate to the neck of the bladder—not referred to by Mijsberg (cf. his fig. 18). We also indicate some differences in the histological nature of the prostatic isthmus on the pubic side of the urethra.

In the urethra, some specific variations are noted in the region of the colliculus seminalis.

ACKNOWLEDGMENTS

We tender our best thanks to Major A. N. Weinman, O.B.E., for material from the Dehiwela Zoological Gardens, Colombo, and to Professor P. K. Chanmugam of the Medical Faculty, University of Ceylon, in whose department part of the work was done. We also acknowledge our thanks to the Council of the Zoological Society of London for facilities and material, and to the Royal Zoological Society of Scotland for material received by one of us (W. C. O. H.) while working in Edinburgh.

We have further to express our gratitude to Miss Bessie Whitely, Guy's Hospital, for the photograph in Plate I (fig. 10) and to Mr. D. Stevenson Clark of Messrs. Ilford Limited, for the photomicrograph (fig. 11).

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10 *Hylobates concolor leucogenys* ♂ newborn.

11 *Hylobates hoolock* ♂ (K.2). Photomicrograph of section through glans penis showing baculum in transverse section. × 50.

nner-Gren Foundation Announcement

Wartenstein Castle, European Headquarters of the Wenner-Gren Foundation for Anthropological Research, New York.

ıe Wenner - Gren Foundation an-
.ces that its European Headquarters
loggnitz, N. Oe., Austria is in opera-
and that 5 conferences were held
ıg the summer of 1959. Dr. Paul
;, Director of Research, invites sug-
ons for future symposia and confer-
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mposia held since the official opening
ıe Headquarters on August 17, 1958

Current Anthropology. Dr. Sol Tax,
nizing Chairman, August 18–24, 1958.
Austrian Symposium, No. 1. *Bei-*
Österreichs zur Erforschung der
angenheit und Kulturgeschichte der
schheit. Prof. Richard Pittioni, Organ-
Chairman, September 8–12, 1958.
Social Life of Early Man. Dr. Sher-
Washburn, Organizing Chairman,
22–30, 1959.

4. *Application of Quantitative Methods in Archaeology.* Dr. Robert Heizer, Organizing Chairman, July 1–9, 1959.

5. *Rural Peoples of the Mediterranean.* Dr. Julian Pitt-Rivers, Organizing Chairman, July 26–August 1, 1959.

6. *Stability and Change in Thai Culture.* Dr. Lauriston Sharp, Organizing Chairman, August 9–16, 1959.

7. Austrian Symposium, No. 2 *Theorie und Praxis der Zusammenarbeit zwischen den Anthropologischen Disziplinen.* Prof. Richard Pittioni, Organizing Chairman, September 6–13, 1959.

Some of the symposia contemplated to take place at Burg Wartenstein during the next two or three summers are listed below, some with tentative titles:

1. *Pleistocene Stratigraphy and Early Man in the Circum-Mediterranean Regions.* Drs. F. C. Howell and A. C. Blanc, Organizing Chairmen, July, 1960.

2. *Comparative Aspects of Human Communication.* Dr. G. Arnold, Organizing Chairman, September 4–10, 1960.

3. *From 15,000 B.C. to the Thresholds of Urban Civilizations—A World-wide Consideration of the Cultural Alternatives.* Drs. R. Braidwood and G. Willey, Organizing Chairmen, Summer, 1960.

4. *Economics and Anthropology.* Drs. B. Hoselitz, R. Firth and S. Tax, Organizing Chairmen, July or August, 1960.

5. *Teaching of Anthropology.* Dr. D. G. Mandelbaum, Organizing Chairman, August, 1960.

6. *Problems in the Evolution and Taxonomy of Higher Primates.* Dr. F. C. Howell, Organizing Chairman, 1961.

7. *African Ecology and Human Evolution.* Drs. F. Bourlière and F. C. Howell, Organizing Chairmen, 1961.

8. *Ceramics and Man.* Dr. F. Matson, Organizing Chairman, 1961.

FOUNDATION POLICIES FOR CONSIDERATION OF PROPOSALS OF CONFERENCES AND SYMPOSIA

TO BE HELD AT EUROPEAN HEADQUARTERS OF THE WENNER-GREN FOUNDATION FOR ANTHROPOLOGICAL RESEARCH, BURG WARTENSTEIN, AUSTRIA

I. Theme. Theme should preferably be along inter-disciplinary lines within anthropology and/or its related sciences: Under this is meant that most or all of the classic subdisciplines (ethnology, archeology, physical anthropology, etc.) should be represented in the conference by subject and/or participating personnel. This policy, however, is not intended to eliminate the single subdiscipline provided the aim of the symposium has a valid inventory or stock-taking purpose. Undesirable are subjects which are termed isolationary on account of high specialization, narrow geographical or chronological limitation. It is a top desideratum that conferences should be of service and interest to the anthropological profession as a whole. Conference themes need not be restricted solely to the anthropological disciplines provided they have the potentiality and prospect of substantially contributin anthropology. They can be based on as the classical disciplines, or any o exact or natural sciences. (Mathemat for example, could be a valid subject i deals with statistics for anthropology

II. Program. No conference prop can be entertained for approval upon t only. A tentative outline of program sh contain suggested titles, the numbe sessions contemplated, as well as the p sible dates.

III. Date. Careful consideration of s able timing in scheduling date and r ning time of conference should be ma It is recommended that proposals for international symposia be submitted preliminary approval at least 12 to months in advance of proposed dat that, if accepted, ample time would b lowed for invitations to be made and pre rations to be carried out.

IV. Participants. Since the Foundat does not believe that any one nation a monopoly on brains or intellectual ca ity, the list of participants should selected internationally and not restric in total or in large part to a single cou Please note that Burg Wartenstein se as European Headquarters of the Foun tion; therefore conferences which ha majority of United States particip should, for financial reasons, be plan to meet in the United States unless travel costs to Vienna can be obtaine the Organizing Chairman from out agencies.

V. Papers. It is recommended conferences should be planned to exc the reading of contributed papers du sessions. Instead, papers should prefer be written, duplicated, and distrib among the participants in ample time fore the actual conference so that par pants have the opportunity to read study them before the meetings be The conference time, then, would be p cipally used for discussion only. Abstra if needed, can always be read by authors during the symposium session refresh the audience's memory.

VI. Publication. It is recommen that papers and results of discussion considered for publication.

I. *Cost.* An approximate and reason- estimate of expenses involved for cipants and prime costs of publication so needed. Please note the travel costs at all times to be based upon the d trip economy or tourist air fare of participant.

ggested sources from which partial ort for travel and publication can be ned, and an indication by the Organ- Chairman of the aid he can render in this respect should be included in the proposal.

VIII. *Approval.* Please bear in mind that the submission of a conference proposal does not automatically mean that the Board of Directors will approve it. For this reason, only tentative invitation to the participants can be made by the Conference Organizer. Upon approval by the Board of Directors, the Foundation itself will issue the final invitations.

k Reviews

PREHISTORIC MAN AND THE PRIMATES. By William E. Scheele. $4.95. World Publishing Co., Cleveland and New York, 1957.

historic Man and the Primates by cheele, the Director of the Cleveland um of Natural History, presents a pic- of primate evolution, with an empha- hominids, in three major portions: al considerations, modern primates, ossil and modern racial evidence for n evolution. Designed for interested s and high school students, the book tten simply, with a minimum of tech- terminology, but without much "writ- own."

hough the book exhibits a number of interpretive fallacies, most of these lso found in many of the writings of ssional zoologists and physical an- ologists, as in the tendency to assume most fossil forms must lie precisely ain phylogenetic lines. There is also implicit acceptance of orthogenesis for *Homo*, Weidenreich's convergent tionist interpretations. Certain con- such as specialization (pp. 16, 19, 8), have been very distorted, while interpretations, such as a southeast or northern Indian center of dis- l for man (pp. 84–85), seem less ble than alternatives. There are, furthermore, quite a few invalid state- ments, such as the restriction of reason to *Homo sapiens* (p. 18) and the assertion that the Piltdown assemblage "conven- iently rounded out part of the human evo- lution story" (p. 28). Scheele's terminol- ogy is generally satisfactory, with unfor- tunately some notable exceptions (pp. 72, 78, 113). In general, the abundant illus- trations are excellent, but too many are misleading (p. 12), non-representative (pp. 61, 117), at least in part erroneous (pp. 24, 76, 77, 80, 92, 116), mislabeled (pp. 91, 100), or almost completely fanci- ful (pp. 29, 76, 81, 88). Many direct copies of drawings and photographs in previously published works are not credited.

But most of the book, written by a semi- professional, is fundamentally sound. It will undoubtedly stimulate laymen and students to greater interest in primatology. Any future edition should be edited, how- ever, by a professional physical anthropol- ogist, and the price should, if possible, be reduced.

William E. Edwards
University of Pittsburgh

THE TRANSVAAL APE-MAN-BEARING CAVE DEPOSITS. By C. K. Brain. 130 pp. Transvaal Museum Memoir No. 11, Pretoria, 1958.

nains of the South African ape man, in caves of the Precambrian Trans- dolostone, have been studied (Dart, n, Robinson et al., 1924–1956). The gical aspects have been somewhat cted. This environmental study was sted by Robinson.

e first part (48 pages) deals with the ble origin and development of the bone-accumulations and fillings, vith methods for angularity measure- ments of sand and for studies of cave breccias and climatic deductions from the deposits. In the second part are treated the findings at Sterkfontein, Makapan Limeworks, Swartkrans and Kromdraai. Climatic placement is attempted, based on faunal evidence given by Ewer (1956). A detailed faunal list follows the report.

Cave fillings are grouped in travertine, residual earth, Phase One and Phase Two materials. The residual earth represents

the insoluble fraction of the dolomite left behind when the cave was dissolved out. Phase One material contains excessively angular residual grains and worn grains from the surface. Phase Two material consists of surface material, brought in when the entrance to the cave was large. Only Phase Two materials are used for climatic deductions. The rate of accumulation of the material has influenced the carbonate content of the final breccia. This fact is taken as an indication that the lime was supplied by percolating solutions and not from the surface as dust. Sand grain measurements based on the porosity of compacted samples of 35–60 mesh sand are described. The angularity serves to distinguish Phase One and Phase Two materials. Reproducibility of porosity figures is claimed to be within 0.4%. Chert grains are strictly of dolomitic origin, while quartz grains are wind-blown. The chert-quartz ratio thus indicates the climate, assuming that increasing quartz abundance indicates greater aridity. Hence fossil dolostone soil should indicate the climate of the time of its formation. It is admitted that no other dating technique than the interpretation of fossil fauna can be employed. Work on fossils led to age determinations ranging between upper Pliocene and upper Pleistocene (Broom). Robinson (1952) presented faunal evidence that the deposits were formed in a series in time and suggested upper Pliocene as most logical. Oakley (1954) placed the sequence in the Pleistocene Kageran-Kamasian interpluvial. Ewer (1955) supported this conclusion. On account of fossil fauna he established the age sequence Sterkfontein - Limeworks - Swartkrans-Kromdraai. The climatic evidence established in the present paper is superimposed upon this sequence.

The author suggests that the deposits of Sterkfontein, Limeworks and Swartkrans belong to the First Interpluvial, while Kromdraai dates to somewhere in the Second Pluvial of Pleistocene time. The evidence is in part controversial. Kromdraai is placed in a wet period although the chert-quartz ratio indicates a trend towards drier conditions, which is not borne out by the porosity measurements. Climatic instability is given for explanation, but Ewer's suggestion of a climate w than the modern one at Kromdraai probably considered. It is not expl why the age of this site then is plac the Second Pluvial.

Several stones with apparent arti fracture have been found. The au states that the damaged stones are safely determined artefacts. His p graphs show only one view of the st so that the profile cannot be judged. he used these controversial objects a endorsement of an age younger Kageran of the deposits, though it is apparent why. No trace of stone cu exists in the lower levels of the dep where most bones including Australop cines were accumulated. An artefact- ing horizon with occasional ape-man mains overlies the main fossil bearing els at Sterkfontein and Limeworks. author believes that the caves may r sent primitive human occupation and that the ape-man did not produce tools, but rather formed the diet of primitive men. Further research is fo to be necessary on this suggestion. F the supposedly arid Limeworks de bones of Hippopotamus are known. author states that these bones need throw some doubt on the suggestion permanent water was absent from the mediate vicinity of Limeworks, "as bones might have belonged to an unf nate wandering individual that cam grief while searching for a suitable p It appears that Ewer's suggested Kag Pluvial age for Limeworks should no discarded too hastily, and that the "c ly interpluvial age of some aridity" Limeworks could be questioned.

No considerations of the paleontolog differences between the ape-man spe of different deposits are given in paper. Yet the studies of Robinson m point out that a time gap exists betw the Australopithecus deposits of St fontein and Limeworks and the you Paranthropus deposits of Swartkrans Kromdraai. There are marked differe between the two species, and diffe food habits have been suggested. fractured rocks were found only on of Australopithecus bearing deposits are not reported from the Paranthro

Therefore paleontological reasons ate a grouping Sterkfontein-Limes and Swartkrans-Kromdraai. Since vidence of extreme aridity at Limes is weakened by the Hippopotamus he humid climate indicated for Krom- rests on controversial sedimentol evidence, the placement of the three in the First Interpluvial and of Krom- in the Second Pluvial must be coned highly tentative.

e paper gives a very thorough comon on the origin and development of Transvaal caves and their deposits. The techniques of investigation are carefully explained, yet not necessarily free of pitfalls in their application. Controversial evidence has not been exhausted sufficiently, and the correlation between faunal age and climate is not the only one possible. The author treated the geological aspects of the problem admirably. Perhaps other means should also have been employed besides sedimentological techniques, as there are pollen and trace element studies.

The paper is highly recommended.

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THE DENTITION OF THE GROWING CHILD: A Longitudinal Study of Dental Development Between 3 and 18 Years of Age. By Coenraad F. A. Moorrees. vi + 245 pp. $5.50. Harvard University Press, Cambridge, 1959.

is treatise represents the second c contribution to be published by this r wtihin the space of two years, and s predecessor, "The Aleut Dentition," ind a wide anthropological audience. ugh of prime interest to the orthost, those concerned with the growth levelopment of children will also find volume to be of singular value. This demonstrates not only an intelligent ach to the study of growth and development of the dentition, but a refreshingly st awareness of many of the limita- inherent in the material. The prestion is straight-forward and concise. ntrast to the earlier work, Moorrees laced the figures in context with the ssion.

e material studied consisted of the r casts of the dentitions of 184 North ican White children. The investigas intentionally restricted to measure- of growth changes in the dentition r. Casts were taken yearly, or in some every six months, from the ages of r three years to 16 or 18 years. How- it is regrettable that gaps of at least rs occurred in most of the series be- the ages of 12 and 16 years. These were obtained as the result of the ined support and efforts of several orations. The majority (132 children) nated from the longitudinal studies of child health and development of H. C. Stuart, Department of Maternal and Child Health, School of Public Health, Harvard University, assisted by F. G. Allen, J. M. Gable, and P. Williams. The remainder were collected in a Wilmington, Delaware, school by R. H. Stucklen.

The stated objective of this study was to emphasize "growth changes in each individual child in order to gather basic information applicable to clinical diagnosis and prognosis in dental practice." A longitudinal approach was utilized since this method "affords an opportunity to study the developmnt of individual children, because it recognizes the individual as the primary unit of study." However, the author states, "Nevertheless, longitudinal studies may yield no more profitable data in terms of the individual than cross-sectional studies unless specific methods are employed to determine the individual patterns of, and variations in, developmental progress."

Preceding 11 chapters of this work is a 39-page review of the literature which traces the " . . . close chronologic parallelism . . . from the realization that the subject of orthodontics, as 'straightening of the teeth' its now generally called, is inseparably linked with growth and development." Although the literature cited is not claimed to be complete, several im-

portant references, such as Jørgensen's work on the deciduous dentition, Schour and Massler's developmental studies, Garn's eruption investigations, Sakai's dental arch studies of the Japanese, and Krogman and Sassouni's syllabus, were conspicuously absent from references cited.

Of interest is a unique "composite graph" designed to provide a graphic record of the various observations on tooth position and occlusion for each child. Features are recorded in three planes. Horizontally recorded data concerns interdental spacing, shape of the maxillary and mandibular dental arch, and molar or premolar crossbite. Observations which are recorded in the sagittal plane include occlusion of deciduous second molars, permanent first molars, and distance between maxillary and mandibular incisors, as well as plots of occlusal plane of incisors, molar, and premolar groups. Vertical overbite was recorded in the vertical plane. Sexual differentiation in age of tooth emergence necessitated separate composite charts for males and females.

Other chapters deal with methods for determining norms of dental development, dental arch size, mesiodistal crown diameters, spacing and crowding, and overbite. Predicting dental development, dental development in the individual child, the value of longitudinal data for orthodontic prognosis, and some clinical applica of the findings will be of particula terest to those engaged in clinical as A detailed appendix enumerates length, arch breadth, and available sp data upon which the conclusions are b and an index is also given.

There are many limitations to this st but as the author has pointed out, it wo take at least 15 years to gather a bo data more satisfactory. The author scientiously attempts to point out w nesses and unsatisfactory aspects inv in this investigation and does not att to extrapolate or stretch his data. S may question the validity of the mea ments which were taken on casts mad different methods, different investiga and over a considerable period of t However, the dental anthropologists applaud the careful definition of term encountered and explicitly used by th thor, such as crown length and brea which have unfortunately been used biguously in many past investigation

Moorrees has made an important tribution to dental research. This will form a valuable supplement to cou in child growth and dental anthropo as well as being of particular benef orthodontists and other clinicians.

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engel's Deformity and Club-Foot: Anthropological Interpretation

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INTRODUCTION

ıe following theory on the anthropolog- significance of Sprengel's deformity club-foot rests on the evidence of hu- embryology, on the comparative anat- of human races and of the anthropoid Diagnosis of talipes equino varus result of arrested normal development ıe foot has been long recognized by icians; its interpretation as a survival an of his simian ancestors' anatomy more recent concept of anthropolo- As to Sprengel's deformity, although ıigh level of origin of the shoulder- e in the human embryo has been fre- tly described, its bearing on Spren- deformity and on the emergence of :k in man, seem to have aroused little est.

the course of many years, theories to ıin these deformities have been re- ed in my lectures on anatomy to med- students in Washington University. 'ebruary 25, 1952, my paper on "The ropological significance of Sprengel's :mity and club-foot" was read before it. Louis Anthropological Society. Dur- the years following, further observa- and study have increased my confi- e in the theory that these two heredi- deformities are reversions to ances- states and have urged its publication.

REVIEW OF THE LITERATURE

Sprengel's deformity and talipes equino varus

ıe pathological condition named "con- tal high shoulders" in English medical ıture was described by Dr. Otto Ger- Karl Sprengel (1891). Briefly stated, :ases were 4 children, a girl and three , in all of whom the deformity was on left side only. The author wrote that he was unable to find previous reference in the literature to this congenital defect. Following Sprengel's publication, other cases were discovered by clinicians in their practice that confirmed Sprengel's description and added new features observed to the picture he had drawn (figs. 1, 2, 3, 4).

Cases of the deformity affecting both shoulders have been reported, as those of Sick ('02), Horwitz ('08), Blair and Wells ('59, see fig. 5), and others. In these cases a forward projection of the shoulders has been noted. The neck appears unnaturally short on the affected side in unilateral cases; symmetrically short, breve collis (Greig, '24), when Sprengel's deformity is bilateral. The clavicle is inclined upward from its sternal articulation to meet the acromion, whereas its position in the normal adult is nearly horizontal. It has been described as stouter and shorter in contrast to its typical form. The scapula on the affected side in a case of Sprengel's deformity is smaller than its fellow. Its position is higher than normal, the acromion, coracoid process and the larger part of the glenoid fossa standing above the level of the first rib. The scapula is rotated on a superior-inferior axis so that its lateral margin looks anteriorly. The bone is also turned, bringing its inferior angle nearer to the vertebral column. The form of the body of the scapula is altered by the reversal of the ratio of its sagittal length and its transverse breadth: the former being shorter than the latter in the Sprengel's deformity scapula. Furthermore, the supraspinous part of the body is bent anteriorly, fitting the convex wall of the thorax. A large bony or cartilaginous strip or triangular plate (the omovertebral bone) is often present; it articulates with the vertebral margin of the scapula and with the laminae or spi-

nous processes of lower cervical vertebrae, and in some cases also with the first thoracic vertebra. The occurrence of this appendage is in about half of the reported instances of Sprengel's deformity (Bateman, '55). Its nature has been the subject of much discussion.

Shortening and altered direction muscles attached to the scapula are corded. The sternocleidomastoid mus may be short, associated with tortico (Horwitz, '08). That the general soma growth of individuals with Sprengel's formity tends to be below the average

Figs. 1, 2, 3 Sprengel's (1891) original cases.

Fig. 4 Sprengel's deformity in a boy of 7 years, after Mercer ('50).

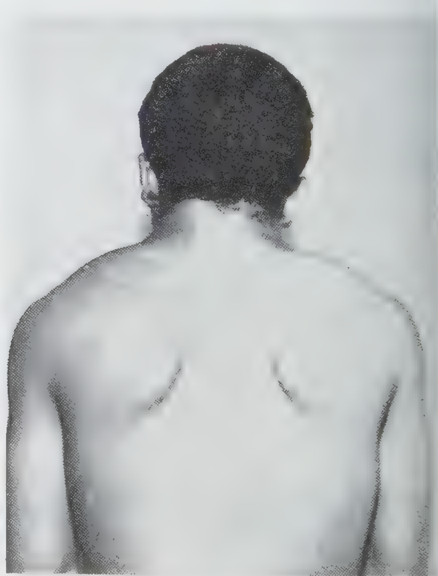


Fig. 5 A bilateral case of Sprengel's deform after Blair and Wells, '59. (U. S. Army pho graph).

observed by Greig ('24). There s to be no predilection of the deform- or race or sex. Regarding inheritance, hof ('13), has reported 7 cases in one ly; Sick ('02), cited two sisters with eral high scapulae. As to the inci- e of Sprengel's deformity, estimates based chiefly on clinical cases which not uncommon; slight degrees, how-

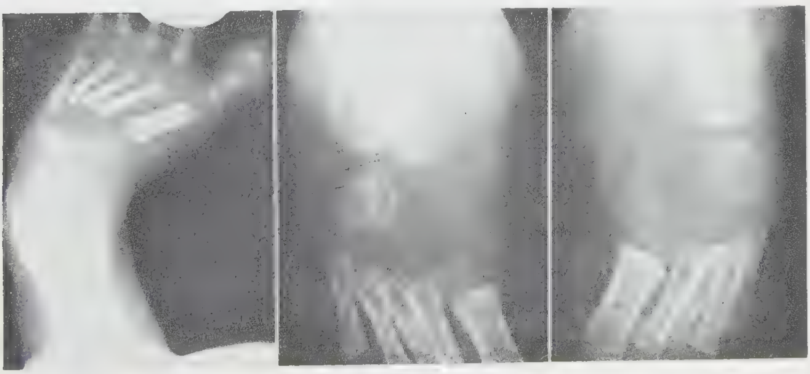
6 Congenital talipes equino varus, right Howorth ('52).

. 7 Bilateral talipes equino varus. Howorth

ever, are unlikely to be included in an estimate of the frequency of this condition.

Putti ('08) recognized the deformity as an arrested stage in normal development resulting from the interruption of the physiological descent of the shoulder-girdle from its high level of origin in the embryo. This migration of the girdle has been carefully studied by Noback ('44). Interruption of the normal migration occurs in connection with the extensive deformations of the fetus so often described, affecting vertebrae, ribs, muscles and other parts, attributed to be the result of infectious disease of the mother during pregnancy (Mercer, '50; Brailsford, '53). In the absence of such an event, however, the normal descent of the shoulder girdle may be interrupted by causes unknown, resulting after birth, in its high position, malformations and functional disturbances that constitute Sprengel's syndrome.

The name club-foot has been given to those deformities characterized by a twisted position of the foot, congenital or acquired. Of the 4 varieties of the former class recognized by the surgeon, that named talipes equino varus is of interest for the anthropologist (figs. 6, 7, Howorth, '52). With this deformity the patient's heel is elevated and the sole is turned inward, that is, toward the median sagittal plane of the body. In consequence, the patient in standing, rests upon the lateral margin of the foot, the heel more or less raised. Walking is difficult and when the deformity is extreme, reduced to a hobble. Talipes equino varus is rarely seen in the adult in the western world today, the de-



Figs. 8, 8A, 9 X-rays of talipes equino varus, from Steindler ('50).

formity having been recognized and corrected early in life.

Concerning the cause of congenital talipes equino varus several explanations have been proposed by surgeons who have had extensive experience in observing and treating this defect. Fechter ('21), quoted by Steindler ('50), noted its hereditary and familial tendencies, recording as many as 5 successive generations afflicted, the hereditary mechanism being of the recessive type. Dittrich ('30) writing on the pathogenesis of congenital club-foot cited its frequent association with spina bifida occulta, its hereditary tendency, and that pes equinovarus is of more frequent occurrence than other types of congenital defects of the foot. Dittrich concluded that club-foot was of neurogenic origin resulting in muscular imbalance in the foot. This author had the opportunity of dissecting an 8-month-old still-born infant having the deformity. Browne ('34) claimed that talipes equino varus is the result of uterine pressure. Raybuck and Manter ('56) reported a case of congenital club-foot in an adult negro.

The following is a brief recapitulation of the important embryological investigation of the human foot by Böhm ('29) taken from Blount's ('29) translation from the German. The foot in 5 stages of its normal development was studied from sections and from wax-plate reconstructions of the skeleton by Born's method.

First stage. Embryo 18 mm C.R. Skeleton cartilaginous, excepting mesenchymal metatarsal I; the small calcaneus is at the lateral side of the talus, both obliquely placed in a direction from proximal-lateral to distal-medial; the navicular juts medially from the margin of the foot; the cuboid lies nearly in line with the fibula; the cuneiforms are progressively larger toward the fibular side of the foot; metatarsals V–II diverge from one another; metatarsal I diverges from the medial side of cuneiform I. The entire foot is flat, is in marked equinus with 90° plantar flexion and in adduction due to the medial inclination of the calcaneus and talus.

Second stage. Embryo 20 mm C.R. The dorsum of the foot is convex, the plantar surface concave; equinus, 90°; the foot is in marked supination; abduction of metatarsal I, and to a less extent of the other metatarsals, is maintained.

Third stage. Embryo 35 mm C.R. The foot is rotated 90° in supination and dorsiflexed; both the talus and the calcaneus are still in slight equinus; there is transverse arching dorsally of the tarsus and metatarsus with corresponding plantar concavity.

Fourth stage. Embryo V, 57 mm C.R., at the end of the third month. The feet are approximated, the soles in contact at the mid-sagittal plane of the body, in slight equinus and still in mid-supination; metatarsal I and the big toe are abducted from the mid-axis of the foot. *Embryo VI,* two weeks older than embryo V, represents a new stage. The bones are showing similarity to those of the adult; the talus is not much altered. The tarsus is further narrowed anteriorly by approximation of the medial and lateral margins and deepening the plantar hollow of the arch of the foot transversely; the plantar concavity of the metatarsus is narrower and deeper; a line through the heads of the metatarsals inclines cranially from the lateral to the medial side at an angle with the horizontal of 45°. The foot is now inclining toward pronation, a process identified with the fourth stage, which continues through fetal life and early infancy.

Böhm concludes: " . . . a severe club-foot resembles an embryonic foot at the beginning of the second month. The only explanation for the great majority of cases of congenital club-foot is the theory of primary endogenous disturbance of the embryo, an arrest of development." Böhm noted that it is hereditary, 4 times more frequent in males than in females.

Lazarus (1896) and Weidenreich ('...) observed the likeness of the crouching and climbing primate foot to the form and position of the embryonic human foot. Changes of the latter in form and position during its development were considered phases in the transformation of a climbing, primate foot into the characteristic human standing and running foot.

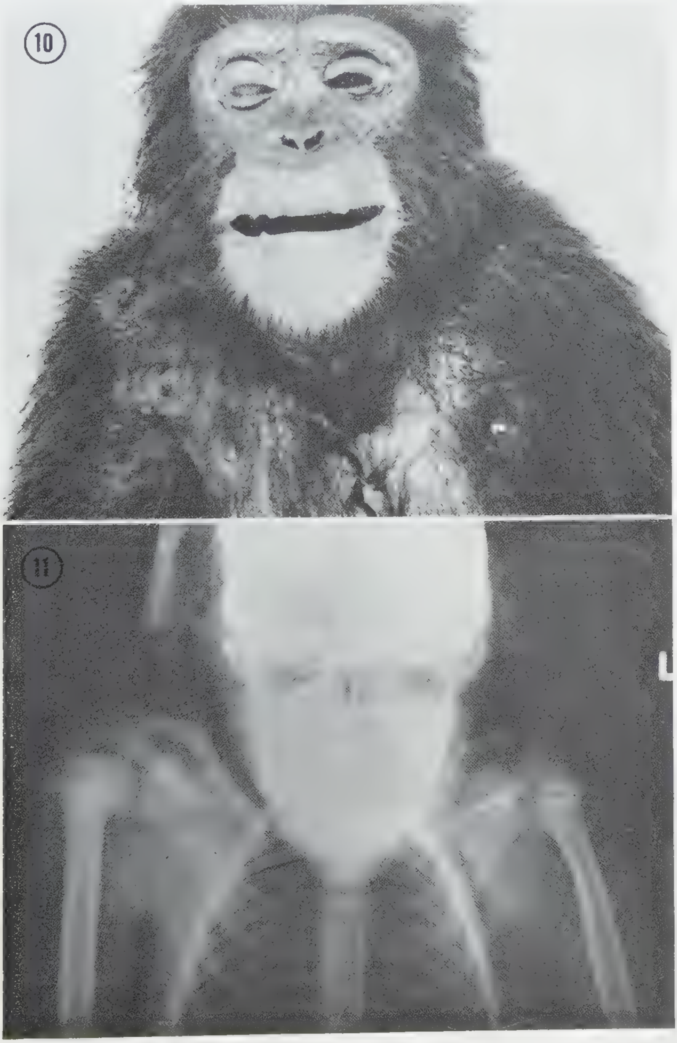
II. The great apes

Bodily proportions of the great apes contrasted with those of man reveal at a glance a short neck, high level and ...

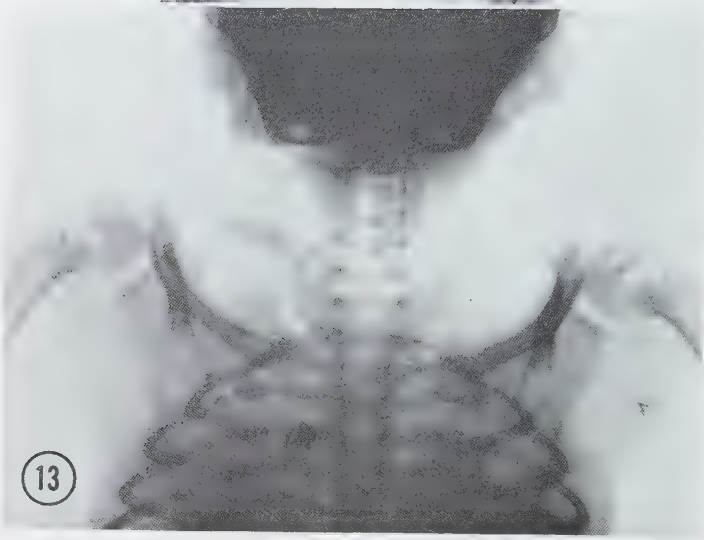
l inclination of the shoulders, long r limbs, long trunk and short lower s. A short thumb is apposable to the fingers from which it is widely sepa- l; the 4 lateral toes are long; the oe participates in the prehensile func- of the inverted foot (fig. 16).

ie neck and shoulders (figs. 10–16). ching for records of measurements of -length, both of man and of the great , I have found very little in the avail- literature. Yerkes ('29, p. 389), has d with regard to the neck in the gorilla there is "no obvious line of demarcation between head and trunk." In Raven's Anatomy of the Gorilla (Gregory, '50), a neck-length of 221 mm is given. According to Keith ('29), the length of the male cervical spine in percentage of the length of the spinal column is: in orang 26, human infant 25, chimpanzee 23, gorilla 23, gibbon 20, adult man 22. These skeletal dimensions are quite different from the surface measurements of the length of the neck.

The surface appearance of a short neck in gorilla was noted by Raven and is shown in plates 7 and 29 in his monograph. The



Figs. 10 and 11 Photograph and x-ray of the head and shoulders of the cadaver of a chimpanzee 18 months old (Terry).



Figs. 12 and 13 Photograph and x-ray of head and shoulders of the cadaver of a young adult gibbon (Terry).

apparent shortness, or absence of a neck in a front view, is characteristic of gorilla, chimpanzee, orang and gibbon. This state in the apes is not comparable to that in cetaceans, in which mammals fundamental changes in the cervical spine, musculature and viscera are presented, resulting in a real reduction in length of this region.

In the apparent short neck of the great apes the sternocleidomastoid muscle holds a position approaching the horizontal in contrast to its obliquity in man. Regarding the origin of this muscle, Schultz, referred to by Robinson ('50), observed the variability of the mastoid process in pongids in which it is absent in the infants, but sometimes present in adults, especially in the aged.

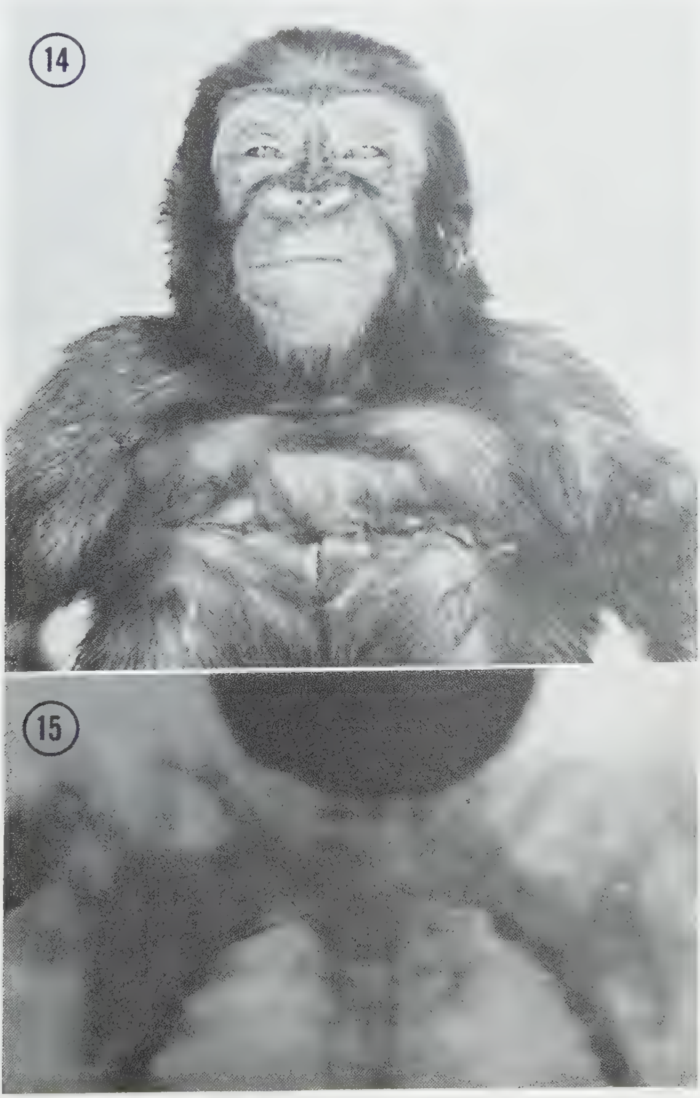
Additional data on the shoulder-gir of the great apes are included in sect IV, Personal Observations.

The foot (figs. 6–9). Martin (' p. 1171) points out the contrast in b the calcaneus and talus between man a the apes in adaptation in the former, their function of supporting the wei of the body in standing on the grou in the latter, to the function of climb in the trees. The sustentaculum tali large in the apes, compared to its size man, the size being in direct relation the variation in the size of the angle the collum tali. This, in turn, depe upon the direction of the long axis of big toe. In adult man, generally, this a of the big toe is nearly parallel to that

other toes, whereas in the apes it di-
;es at a large angle.

he scansorial foot of the ape contrasts
ı the plantigrade human foot in the
er degree of its medial rotation on a
gitudinal axis. This fact has been ex-
ssed by the results of measurement of
angle made by the long axis of the
er calcanei with the vertical. The angle
etween +14° and +30° in apes; in
nan races, +18°, in Wedda; −16°, in
Melanesian; −6°, in European (Martin, op. cit.).

An important difference between the foot of Hominidae and of Anthropomorphidae, cited by Poniatowski ('13) (Martin, op. cit.), is in the size of the angle made by the neck of the talus, which is directed medially from the body of the bone. It measures in *Hylobates* 31.3°; in *Gorilla* 34°; German 20.8°; Maori 23.2°; Australian 25°. According to Volkof (Mar-



Figs. 14 and 15 Photograph and x-ray of head and shoulders of the cadaver of a young gorilla (Terry).

tin, op. cit.), the angle measures in the newborn European 25° to 35°, interpreted as a pithecoid condition. The same investigator found the torsion angle of the head of the talus small in Anthropoids (*Gorilla* 18.7°), in contrast to adult man (40° in Europeans), but in newborn Europeans the angle measured only 16.5°, interpreted by the author as evidence of ontogenetic recapitulation of primitive conditions. The talus of apes is a depressed, somewhat flat bone, in contrast to the human talus. The long axis of its trochlear surface is nearly parallel to the sagittal plane, whereas the long axis of the calcaneus, produced anteriorly, passes through the third toe and is, therefore, the long axis of the foot. Wells ('31) has shown that if these two axes intersect behind the foot, the angle made by them is plus in sign and the axis of the foot is directed outward from the sagittal plane; if they intersect in front of the foot, the angle is negative and the axis of the foot is directed inward. Wells found the angle to be negative in all primates excepting man.

Discussing the relative lengths of the cuneiform bones, Wells questions the prevalent assumption of the second cuneiform being shortened and suggests that it is the lengthening of the first and third cuneiform bones that has created this impression. Recession of cuneiform II is, as Wells shows, a character widely and apparently irregularly distributed among the primates.

Concerning the divergent hallux of the great apes, Morton ('37) refers to the measurements made by Schultz ('34) on the feet of the chimpanzee, the lowland and mountain gorilla, as showing "a progressive reduction in the angle of abduction."

Climbing and walking. That walking in a more or less erect posture is practiced in the trees by the anthropoids is well known. But in this form of arboreal locomotion the balance is assured through the grasping of branches by the feet as well as by the hands. Writing of the chimpanzee on the ground, Wood-Jones ('26) records its ability to walk erect for short distances, but that generally it walks on hands and feet. Yerkes (op. cit.) quoting Schlegel and Müller with reference to the orang-utan's walking on the ground on all fours, says in conclusion, "Prefere for the upright position . . . is wholly a entirely lacking."

Morton ('37) writing on the adopti of a terrestrial habitat by the anthropoi describes how the changes in locomoti affected the arboreal usages of hands feet: a change from locomotion by ar and hands to one by legs and feet, fr vertically suspended posture to vertica supported posture; placing heel to grou and ending of the foot's grasping functi The weight of the body falls upon inner border and the foot is flattened.

III. *Recent man*

Among the contrasts between the figu of man and that of an anthropoid appears the difference in the level of th shoulders. In the ape they stand so hi as to give the appearance, when view from in front, of the head sunken do between them, the neck concealed. adult man the head is elevated well ab the shoulder level revealing the neck. acromial height in the anthropoid ape a greater percentage of the total sta than it is in man. The lower acrom level in adult man has been reached the descent of the shoulder-girdle fr its original high position in the embry A result of this descent is the exposure the neck (figs. 17, 18). The neck i conspicuous, measurable feature, pres ing one of the most striking contrasts be tween man and ape and deserving of ta nomic recognition. See fig. 16, Wilder,

Anthropologists have met with diffic ties in measuring the neck, as one understand who tries the operation by three methods adopted (Martin, op. c p. 158), viz., numbers 29, 29(2) and for neck length. Measurement number is the neck length between the level of spine of the 7th cervical vertebra and inion. In adult Europeans, Oeder, quo by Martin (op. cit., p. 383), gives for called well proportioned men, lengths more than 12 cm.

The neck of the newborn white inf in repose is not visible from in front. descent of the shoulders has not reach at the time of birth a level that wo expose the neck anteriorly. The pho graphs of young children in Gesell's tr

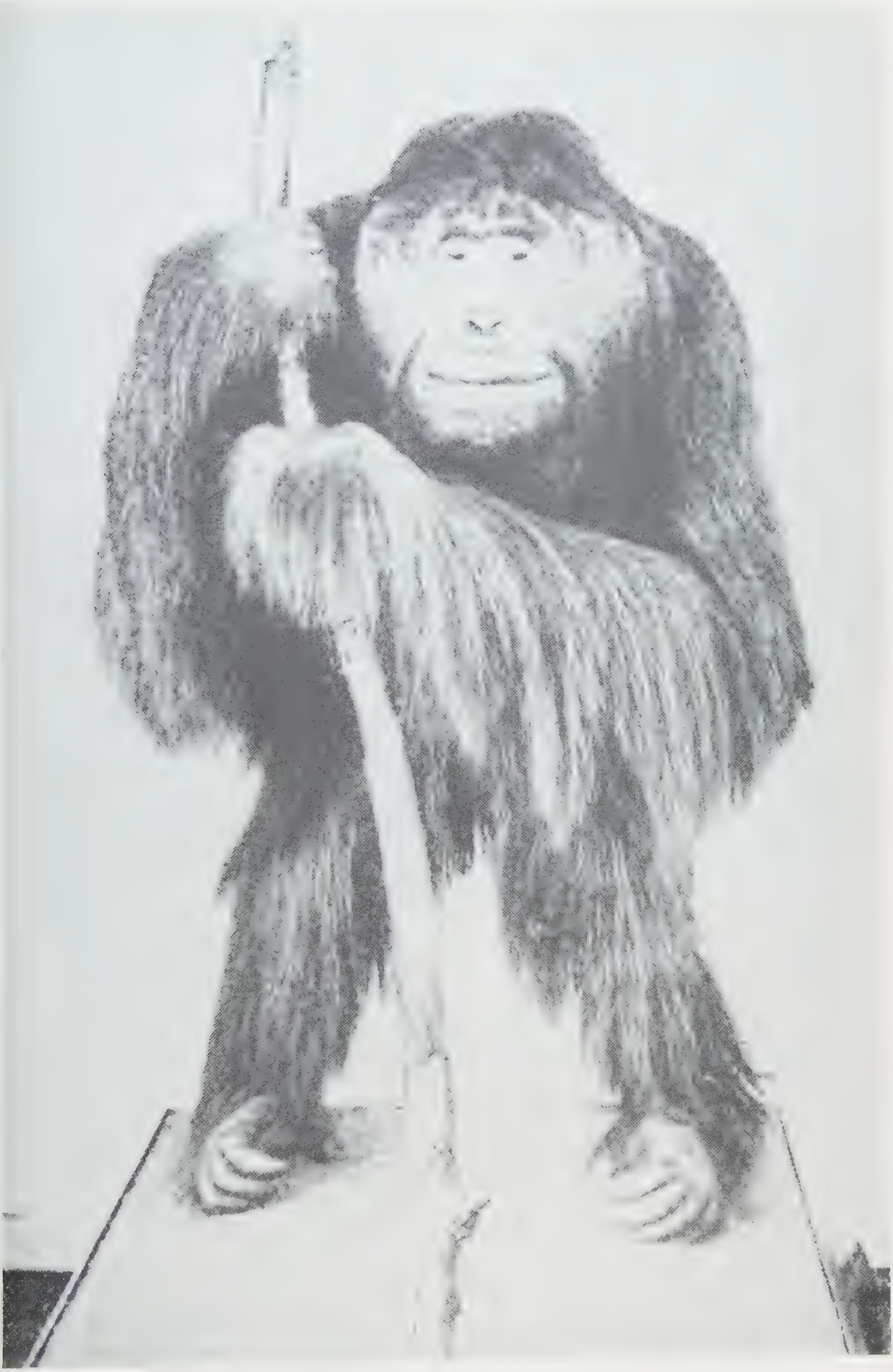
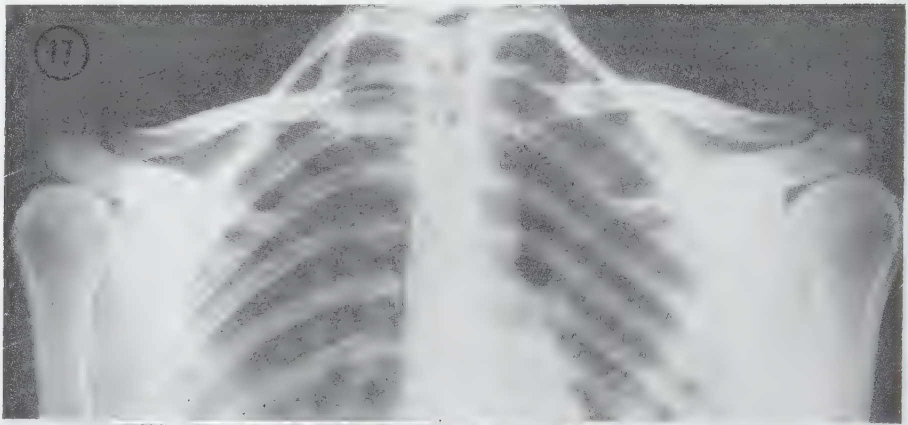


Fig. 16 Orang-utan (From Wilder, '26).



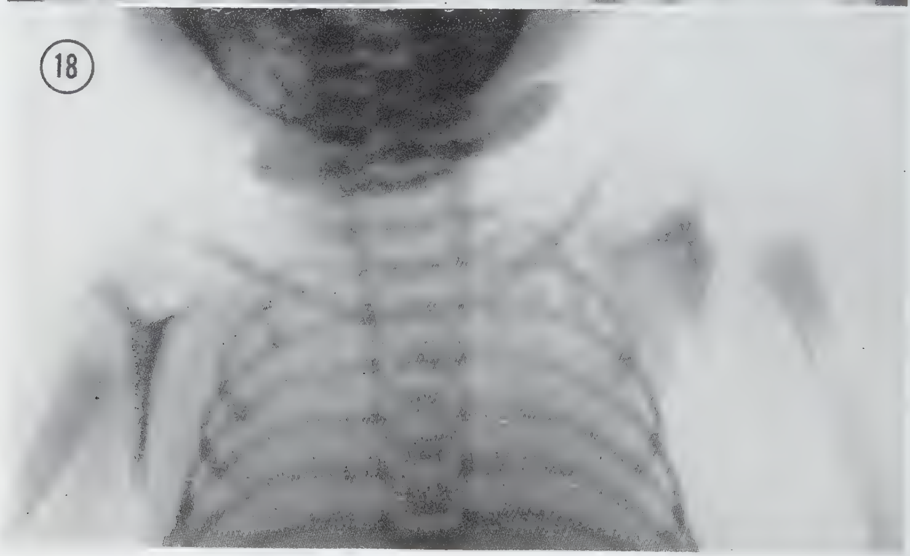


Fig. 17 X-ray of the neck and shoulders of a normal adult white male; from Meschan ('59).
Fig. 18 X-ray of the same regions in a normal newborn white female (Terry).

tise ('34, vol. II, p. 677) reveal the shortness of the emerging neck.

Since at the time of birth the neck is concealed from in front by the jaws, my application of the measurement No. 2, 3 (1), suprasternale-gnathion (Martin, op. cit., p. 158), resulted in a negative value. It is during the first year, when the infant is beginning to raise its head, that the neck is first revealed from in front. The progress of downward migration of the shoulder-girdle continues until about the age of 4 years. This figure is based on too few observations and is to be understood as tentative awaiting opportunity for investigation. However, even in my limit number of subjects, it was observed th there was variation in the levels of desce ultimately reached by the shoulder-gird and confirmed by measurement of the va ation of the angle made by the clavic with the horizontal plane, such as wou account for the familiar differences o served in neck-length. What other facto there may be that determine neck-leng in man, the range of shoulder-girdle m gration is in the first rank of importan and of unique significance in human ev lution. See figs. 17, Meschen, '59, and 1

Fig. 19 Neck as depicted in the Madonna by Raphael.

he head resting between the shoulders, racteristic of the infant, has been faith- y recorded in the paintings of some he great artists of the Renaissance as as in the works of modern artists. h shoulder level of infants and the er shoulders of adults are portrayed, example, in Raphael's Madonna and enoir's Mussel Gatherers (figs. 19 and

If we can accept the accuracy of the sculptor of the head and neck of the Egyptian Queen Nefertiti, 18th Dynasty, a long range of descent of the shoulder-girdle may be inferred to have produced the extreme length of her neck. On the contrary, the migration may be interpreted as having been interrupted in the case of the Sioux Indian Chieftain named "No-Neck," referred to in Stanley Vestal's "Sitting Bull"; and, from Shakespeare's de-

Fig. 20 Neck as shown in the "Mussel Gatherers" by Renoir. Courtesy of the Durand-Ruel Gallery, New York.

scription, also, in the English King Richard the Third: "Deformed, unfinished, sent before my time into this breathing world"; two leaders in their time and place, both probably subjects of Sprengel's deformity.[1] Many photographs of American Indians show a short neck. As a part of the picture of this interesting condition is the extreme obliquity, approaching the horizontal, of the sternocleidomastoid muscle and the rudimentary state of the masto process, both suggestive of simian anato (see in this connection Schultz, '34).

[1] Sir Thomas More's description of King Ri ard the Third (1543) is quoted by Kendall (' '56), Appendix II: "little of stature, ill-featu of limbs, crook backed, his left shoulder m higher than his right, hard favored visage . . . ; he came into the world feet f ward . . . and (as the fame runneth) also untoothed."

. 21 Normal inversion of the feet in the infant, from Gesell ('34).

ne omohyoid muscle in the neck and lder of man, poses questions concern- its phylogeny, innervation and func- , of interest to the anthropologist as as to the student of comparative anat- However, as pertaining to these fields quiry, my review of the literature of shoulders and my personal observa- tions of cases seem to offer little to record and discuss at this time.

In section II certain features of the shape and structure of the human foot have been compared or contrasted with those of the foot of the great apes. In the present section some of the published observations and conclusions on the human foot in its functions of climbing and walking will be reviewed. Fig. 22, Keith, '29.

Weidenreich ('22) writes that it is now generally accepted that the human foot is a climbing foot with the characteristics, more or less, shown by the living Primates. This conclusion emphasizes especially the hallux of man, its form and the position of its skeletal elements, its musculature, its original plan of an apposable toe (figs. 21 and 22). From the climbing arboreal beast, has come the erect standing, walking and running terrestrial man. In walking, the typical climbing beast holds a squatting posture that favors the spring when climbing begins. (How like the position of the athlete at the start of his fifty yard dash!) In summary, Weidenreich concludes that man's standing foot has evolved from a climbing foot.

Straus ('27, p. 132) wrote of the structural resemblance of the foot of the human

Fig. 22 Footprints, adult white males, from Keith ('29); a, normal (high arch;) b, normal (moderate arch); c, low arch; d, flat-foot.

fetus to that of adult arboreal apes as suggesting "a recapitulation of ancestral conditions."

Wood-Jones, in his book, Arboreal Man ('26), a work rich in observations, compares the climbing of the higher apes and of primitive man (p. 66): both using the outer side of the foot and the big toe to clasp the branch, the foot inverted. Concerning arboreal activities of modern man, this author cites (p. 207) the white man's practice of shinning up a pole, of the use of climbing irons; (p. 208) how "unbooted races" have learned mechanical ways of assisting the foot-grasp by using a hoop encircling the tree and the man's waist, compensating for the shortness of his arms (figs. 23 and 24, from Johnston). Wendt ('56), shows in his plate 27, South Sea Islanders walking up a palm tree to "smoke out" a bee's nest and cites a similar method practiced at the present time by honey gatherers in the Provence Valencia, Spain.

Inversion of the foot is a normal a tomical characteristic of the newborn Eu pean. Wood-Jones (op. cit., p. 205), w ing on the normal inversion of the infa feet, tells how the soles can be pres against each other; that when walk begins, it is upon the lateral side of soles; to this inherited position is due earlier wearing-out of the lateral part the sole of the shoe.

An important contribution to our kno edge of human locomotion was made Hrdlička in his book "Children who R on all Fours" ('31). One subject, a gro woman, is quoted as having practi quadrupedism since childhood. This man, with knees straight, could turn feet inward and place their soles in c tact.

Fig. 24 Padung Malay, Sumatra, climbin tree by the aid of a rattan rope (tali amb This figure and figure 23 both from Sir H Johnston, "Living Races of Mankind."

Fig. 23 "Tree climbing in Australia by a "Black Fellow."

oollard ('38), as recorded by Gates p. 142), reached the conclusion that nodern type of man was present in arly Pleistocene.

IV. Personal observations

oulder-girdle and neck in man. In Atlas of Thomas Dwight (1881), zen Sections of a Child" (Whose age said to be three years), there is shown ate II the acromion and clavicle, part e body of thoracic vertebra I and the of thoracic vertebra II; also parts of I and II, the body of the scapula and apices of the lungs, but no trace of manubrium sterni; all of these parts g evidence of a higher level of the lder-girdle in this child than obtains ally in the adult.

diographs of 10 still-born white in- and two fetuses from the Department natomy, Washington University Medi- School, showed high levels of the lder-girdle in all, the clavicles inclined ard and laterally at varying angles the horizontal plane (fig. 18).

y endeavor to measure and record the ress of the downward migration of shoulder-girdle and the time of its ination, revealing the neck in its ulti- extent, was interrupted and at this ent I can present evidence of the omenon only by reference to the por- ure of the neck as shown in the paint- of the two great artists mentioned e (figs. 19 and 20).

oulder-girdle and neck in the great . I am indebted to the St. Louis Zoo- cal Garden for the opportunity of study- the following three specimens of great after autopsies had been performed he Gard n: Gorilla (*Gorilla gorilla*), ale, about two years; Chimpanzee (*Pan npanzee*), male, 18 months; Gibbon *lobates lar*), female young adult.

In the preparation for making photographs and roentgenograms the subjects were posed on their backs, arms at the sides of the trunk, face looking forward. Referring to figures 10–16, it will be seen that the high level of the shoulders and the apparent reduction in the length of the neck in these apes is in striking contrast to these features in man. The x-ray has recorded the inclination of the clavicle from its sternal articulation laterad and cephalad, as Hill ('57) has observed. The level reached at its acromial articulation, varying somewhat in the pictures between the right and left sides, is, in contrast to its level in man, high above the plane of its sternal articulation. The clavicle of the gibbon is robust and markedly curved, a true "collar bone;" that of the chimpanzee slender and sigmoidally curved; of gorilla, short and thick. The body of the scapula in the three apes holds a high position on the back commensurate with that of its acromion. The place occupied by the human shoulder blade is upon the dorsal wall of the thorax between the levels of the second and seventh ribs; the cephalic (upper) margin of the body of the scapula in the three apes under consideration is well above (cephalad) the first rib. The level of the shoulder joint is higher in these apes than it is in adult man, thus contributing to the range of their upward reach, an obvious advantage in climbing.

Sprengel's deformity and club-foot, concomitant. The occurrence of Sprengel's deformity and congenital talipes equino varus in the same individual must be very rare in the practice of orthopedic surgeons. My search for this possible association, both in the literature and through inquiry of practitioners has met with no success, with one exception. This experience is strange in view of the fact that

TABLE 1

Angle of the cephalo-lateral inclination of the clavicle made with the transverse plane (Apes and Man)

	Age	Sex	Right	Left
Gorilla	Young	Female	48°	40°
Chimpanzee	18 months	Male	32°	30°
Gibbon	Young adult	Female	52°	40°
Man	Newborn white	Female	47°	30°

high shoulders and inverted feet are normal concomitant features of the fetus and the infant.

The single example found in my search for a case presenting a picture of these embryonic rests, at an age later than infancy, was that of a 5-year-old white boy. He had been brought to the St. Louis Shriners' Hospital in the fall of 1955 for treatment of a unilateral Sprengel's deformity. He was well nourished and responsive. Inspection revealed asymmetry in shoulder levels, the left higher than the right. By palpation the left scapula was found to be 1.5 inches above the level of the right. X-ray revealed the left scapula smaller than its mate, its position nearer to the vertebral column and rotated on a vertical axis. The patient, placed on his back, his feet bare, presented a quite marked talipes equino varus of the left foot.

SUMMARY AND COMPARISON

The text of this paper to the present point has been a descriptive review chiefly of the anatomical characteristics of the shoulders and neck in Sprengel's deformity, and of the feet in talipes equino varus, derived from the literature of these subjects; and a review, likewise, of descriptions of the anatomy of the shoulders, neck and feet in the great apes. Some observations of the author on the same subjects are recorded. It is proposed now to compare these deformities in man with the normal constitution of the homologous parts in the apes.

Sprengel's deformity. Inspection of figures 1–5, presenting typical cases of Sprengel's deformity, and of figures 10–16, the normal shoulder-level in the 4 great apes, shows the conditions strikingly alike in several respects. Bilateral Sprengel's deformity, it has been noted, is not rare in its occurrence. The forward projection of the shoulders in these cases is a simian characteristic. Concomitant apparent shortness of the neck, dependent upon high shoulder level, obtains in the deformity as it does normally in the ape. In the uncomplicated Sprengel's deformity, as in the ape, there is no real shortening of the cervical spine. As revealed by x-ray, the level of the shoulder-girdle in the deformed subject is high above its normal posit
the acromioclavicular articulation
above the level of the first rib. The c
icle holds an oblique position, as in t
ape, in contrast to its normal nearly h
zontal state. These observations conc
ing the position of the shoulder-girdl
cases of Sprengel's deformity match th
made on gorilla, chimpanzee and gibb
Evidence of the deformity being an a
rested stage in human ontogeny is gi
by the high position of the shoulder-gir
as proved by x-ray in the normal hum
fetus and newborn infant, 12 in num
and in a child of three years (recorde
section IV). Of possible significanc
the shortness of the clavicle observe
some cases of Sprengel's deformity, re
ing the relative shortness of the collar b
of the gorilla. Reversal of the long axi
the body of the Sprengel scapula, cha
ing its shape to one comparable with
of the anthropoid, is an impressive fea
of the deformity. Inheritance of Spreng
deformity in several families is recor

Talipes equino varus. That the nor
human foot presents in its structure m
of the characteristics of the foot of
anthropoid ape has long been recogni
If the likeness is masked or manifeste
only moderate degree in the normal f
its true nature is revealed in talipes equ
varus. In review of the distinctive m
up of this form of club-foot and of
of the normal foot of the great apes,
following features may be compared.
sustentaculum tali, both in the skele
of the ape's foot and in that of a case
talipes equino varus, is large in contras
its size in a normal man, although
talus itself is small and narrow in c
foot. In the deformed foot the head of
talus is directed medially at a grea
angle than normal, and can be regarde
a pithecoid characteristic. In talipes e
no varus the foot is in marked supinat
as it is normally in the ape. The big
of the human embryo, in an early st
of development, is abducted to a deg
approximating that in the adult ape.
may be recalled here that inversion of
foot is present as a normal state in
human infant and that the footprint of
adult European still indicates a degree

rsion (fig. 22). The persistence of ty and natural inclination of man to b can be credited to a heritage of the ts of his arboreal ancestors. Lastly, fact of a hereditary tendency of this rmity, club-foot, is well established.

ie incidence of Sprengel's deformity talipes equino varus in Europeans and h African tribes awaits investigation. ı on stature in the same categories is h to be desired.

CONCLUSION

Theory on the emergence of Homo

is postulated, (a) that the descent of shoulder-girdle, which occurs normal- the human embryo and infant, began mutation in the embryos of some of 's arboreal, simian ancestors, male and ale; (b) that the mutation appeared ie Pliocene; (c) that it became estab- d as a dominant hereditary trait. The ilder-girdle of the great apes does not rgo this migration and retains the level of a fetal state.

s a result of the mutation, the range ie affected ape's arm-reach above the l was shortened by a distance equal to of the downward migration of the ilder-girdle. Also, the range of adduc- of the elevated arms was lessened by encounter with the head. These, and ably other changes from the normal ditary pattern, were followed by fatal equences to skill in climbing and to ortunity for obtaining food in the trees. ape, affected by this mutation, could compete successfully with his fellows suffered hunger. It was more difficult him, so deformed, to defend himself nst his natural enemies, or to escape ı them, than it was for his unafflicted nal companions. The deformity put to disadvantage in finding a mate. affected beast found himself ostra- d, pestered and eventually subjected ttacks by his fellows, true to immemor- custom. Starving and life threatened, abandoned his arboreal home and ght sustenance and saftey on the ind.

looton ('46) presents another reason the ape's exodus from the trees. "Let suppose," that man's ancestors chose to live on the ground, having taken the chance of finding a fuller and a better diet; "they wanted to live their lives more abundantly."

Variation and natural selection changed the arboreal pongid, subject of the mutation, into terrestrial *Homo.* Evolution of the erect posture, already well advanced in his arboreal environment, continued toward perfection in adaptation to the physical features encountered when standing and walking on the ground. The curves of the spine and the backward growth of the skull are responses to the needs for balance.

"If it be an advantage to man to stand firmly on his feet," wrote Darwin (1871), "and to have his hands and arms free, of which, from his pre-eminent success in the battle of life, there can be no doubt, then I can see no reason why it should not have been advantageous to the progenitors of man to have become more and more bipedal. They would have been better able to defend themselves with stones or clubs, to attack their prey, or otherwise to obtain food. The best built individuals in the long run would have succeeded best and would have survived in larger numbers."

The neck of the mutant, now free from the restraint imposed by a high shoulder-girdle, enjoyed a larger range of movement in which the sternocleidomastoid muscle participated (the mastoid process developing concomitantly), so providing for a wider area of vision. Keener twilight perception of dangers on the ground that are not encountered in the trees was imperative. The larynx, located in the head of the ape, as it is in the human embryo, eventually descended into the neck, establishing new relations with the tongue, a possible advance toward articulate communication. The teeth underwent a modification of the crown in adaptation to the greater diversity of food yielded by the earth than was offered by the trees: of vegetable, animal, mineral in abundance. Escape from attack by beasts on the ground was insured by swift return to the trees, the recourse still practiced today by primitive man and his civilized brothers. The brain began its marvelous growth and evo-

lution, stimulated by and in response to environmental dangers, opportunities and rewards.

"As the progenitors of man became more and more erect, with their hands and arms more and more modified for prehension and other purposes, with their feet and legs at the same time transformed for firm support and progression, endless other changes of structure would have become necessary. The pelvis would have to be broadened, the spine peculiarly curved, and the head fixed in an altered position, all of which changes have been attained by man." Darwin (1871).

Dart's momentous discovery ('25a) of the man-ape, named by him *Australopithecus africanus*, was made in 1924, at Taungus, Betuanaland in the Kalahari Desert. It was a child's skull which he found embedded in limestone, probably of the Pliocene Epoch, and because, chiefly, of its greater cranial capacity, 500 cm^3, and of its reduced prognathism, it has been truly judged primitive *Homo*. Dart's discovery urged him on to indefatigable labors that have brought their rich rewards. His work has revealed the structure of one of the primordial ancestors of *Homo*, evidence of his predatory habits, the use of weapons and other implements for obtaining food. From the site at which the relics were found, the edge of the Kalahari Desert, Dart inferred that the Australopithecinae lived in an unforested region much as it remains today.

Following Dart's fundamental discoveries came those of Broom and Schepers ('46), also in the South African region, of like fossils, named by them, *A. transvaalensis*. These ancient types were short in stature in contrast to early *Homo*, as found in *Pithecanthropus* by Dubois (1894) and in *Sinanthropus* (*Pithecanthropus pekinensis*) discovered by Black ('34). This increase in stature over a long period is in accord, with some exceptions, with the history of vertebrate evolution.

The theory here offered on the origin of a part of present day mankind assumes that the occasion of the shoulder-descent-mutation occurred many times in steps over a long period down to the present. The mutation took place in several of the regions where pithecoid remains have b
discovered; I may cite the *Adapi*
Eocene, in North America and Eur
Tarsiidae, Recent, in the East Ind
Papio, Pleistocene, in Africa (Romer, '

It will have been noted that the hyp
esis of the mutation of shoulder-des
has been limited in its application to s
of the simian ancestors of *Homo*, and
it assumes these ancestors were arbo
apes. The discoveries in Africa by D
nan ('45), Dreyer ('32), Leakey ('3
Wells ('37) and of others, present
dence, difficult at the moment of gai
general agreement in interpretation, of
descent of the prehistoric natives of So
Africa from a terrestrial anthropoidal
cestry. The contrast in pattern of the
of the Bantu, Bushman and Hottento
that of a climbing ape has been cle
demonstrated by Wells.

Weidenreich ('22) found little simi
ity between the foot of the anthropoid
that of the Negro, Australian, Hotten
Vedda and Sunda Islander. He conside
that the standing foot of *Homo* has b
derived from a climbing foot, its f
having been changed by pressure on
ground, a process that may lead even
ally to a flat foot. Wells ('31) has
scribed in detail the characters of f
form that mark the Bantu, Bushman a
Hottentot, among them a divergent
toe, that contrast with those of the Eu
pean. Concerning African pygmies, Qu
refages (1895) found the feet flat-sol
and the heels projecting "a little
much." It would be of interest to kn
whether these native Africans are in so
instances deformed by congenital cl
foot as are members of the white race.

The photographs of two African p
mies, reproduced in Quatrefages (189
page 176, reveal high shoulders, short n
and clavicles inclined upward and o
ward. Schebesta ('33), in his descripti
of Congo pigmies, noted a short ne
broad short nose, arms abnormally lo
feet freqeuntly introverted. The avera
stature of Bambuti males was 4 feet,
inches; females, 4 feet 4 inches. T
author regarded the Bambuti as Bushm
with some Boskop ancestry. Pygmies
day, form a not inconsiderable part of t

ılation of the Eastern Hemisphere; racial affinities differ, and some owe dwarfed stature to pathological pro- ɜs. Excluding the last, their stature certain anatomical features, such as ɐ cited above, argue in favor of these people being representatives of a ɜ in the evolution of the genus *Homo*. ıis interpretation Sprengel's deformity be assessed as an atavistic phe- ıenon.

SUMMARY

ıis paper presents evidence in support ıe theories: (1) that the two deformi- of man, viz., Sprengel's high shoulders club-foot, are atavistic of normal con- ıns present in man's simian ancestors; that normal descent of the shoulder- .e, exposing the neck in human on- ıny, began as a mutation in one branch ıan's arboreal ape-progenitors, causing to abandon his arboreal life for a ter- ial habitat; and (3) that the reactions ıriation and environment changed the real pongid, subject of this mutation, terrestrial *Homo*, an experience me- ialized by the scars of Sprengel's de- ıity and club-foot.

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; Determination from the Internal Structure ıe Humerus

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ɛ possibility of determining age from ıternal structure of the humerus was ·vered long ago by experts in legal ɔine in Europe but appears not to be known to American anthropologists vart and Trotter, '54). In view of I have undertaken to summarize y the work that has been done in this

ıchholz (1894) was the first to carry ıvestigations on physiological changes ɛ humerus throughout the life span. udied sections of fresh bone in 230 ranging in age from 8 to 54 years. ıg his findings are the following:

Osseous union of the proximal epi-s with the diaphysis begins at 14 in Viennese girls and at 16 years in ıese boys.

Complete union, i.e., the disappear- of the metaphyseal cartilage, occurs e 17–18 in Viennese women and at l years in Viennese men; at 19 years ·acovian women and at 23 years in ɔvian men.

By the 30th year the linea epi-ıria (sutura diaphysaria) has mostly peared. In other words, this line can-e seen at the surface of a fresh bone it is sawed longitudinally through ıberculum majus.

Shortly after 28 years in females, ıbout 30–35 years in males, the cone ɛ medullary cavity reaches the collum rgicum.

Shortly after 35 years in males, and what earlier in females, the medul-cone reaches the zone of ossification sutura diaphysaria).

ırier ('31) also was of the opinion the linea epiphysaria ultimately dis-ırs and that at an advanced age the llary cavity of the diaphysis commu-es with the caput humeri.

More recently it has become evident that the conclusions of Wachholz and of Poirier are not correct in all respects. It was for this reason that I took up the study of this subject. Working in the Institute of Forensic Medicine of the University in Budapest, mainly in the years 1927–1933, I examined a series of 674 humeri ranging in age from newborn to 106 years. My conclusions are as follow:

1. When fresh bone is sawed and washed, the delicate internal structure cannot immediately be judged with accuracy.
2. The interepiphyseal line can always be detected in macerated humeri regardless of the degree of advanced age.
3. This line is not perforated by the medullary cavity although the latter advances from the diaphysis toward the epiphysis as age advances.
4. In old age an independent medullary cavity forms on the inside of the tuberculum majus proximal to the interepiphyseal line.

As indicated in the first of the foregoing conclusions, I got a far better and more accurate picture of the internal bone structure when the bones had been thoroughly macerated before sawing rather than when the bones were sawed before maceration. No real damage is done to the internal structure during maceration when the bones are intact.

Bruno ('34) reported similar results on macerated and sawed humeri. His roentgenological results are similar also. In his opinion the metaphysis remains visible throughout life but becomes spongy; lacunae are formed in the proximal epiphysis of the humerus after 40.

Berndt ('47) was the next one to consider this matter. He was concerned about the time required for maceration and he

hoped by the aid of radiograms to speed the interpretation of the structural qualities of the bone. His work was carried out in the Institute of Forensic Medicine at Halle and was based on 85 humeri, mainly males, ranging in age from 16 to 89 years. The results of this work confirm and extend my own, giving a more precise determination of age.

I would point out that Berndt's roentgenographs are not quite identical with the appearance of the sectioned humerus. This is due, of course, to the fact that in roentgenograms the entire thickness of the bone is projected on the film (figs. 1 and 2). Comparisons of x-ray pictures with sectioned bones are only grossly similar, the fine structure being divergent. Therefore, age determinations from x-ray pictures are less exact than those from sectioned bones.

In view of the foregoing, radiography of the upper end of the humerus should be used as a method of age determination only when the bones are too valuable to be sectioned. Among very ancient finds it sometimes happens that the intertra lar lacunae are filled with grains of and, hence, yield indistinct radiogr In such cases sectioning of the bo indispensable to further exact inves tions.

In 1953, as a result of the most re investigation of this subject, Hansen, of the Institute of Forensic Medi Humboldt University, Berlin, publish monograph based on 250 macerated meri, ranging in age from 15 to 85 y His experience and illustrations sup the findings summarized above.

All of these findings may now b stated in a chronological arrangement

15–16 years. The metaphysis is cartilaginous.

17–18 years. Incipient osseous u is taking place between epiphysis and physis (fig. 3). The diaphyseal int structure is for the most part ogival.

19–20 years. Epiphysis and diap are nearly united. The internal stru of the epiphysis is on the whole ra

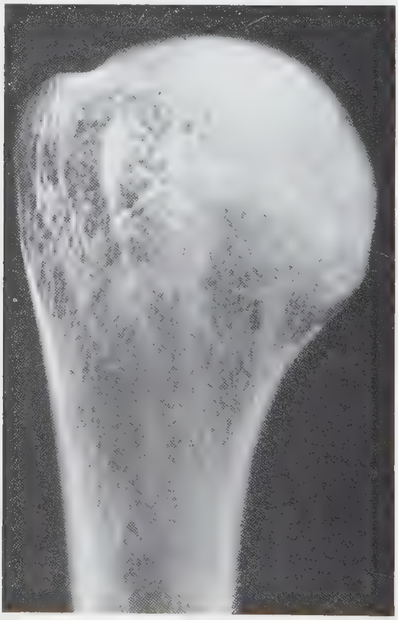


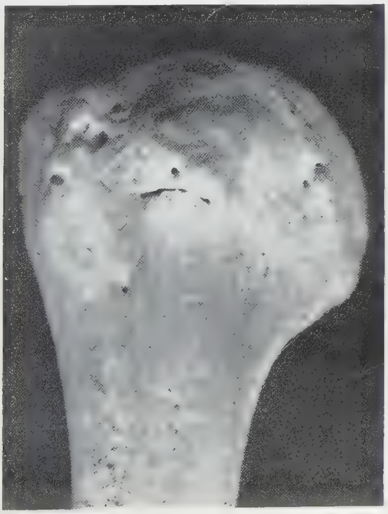
Fig. 1 Roentgenogram of proximal humerus from the Eneolithic period, Tiszapolgár, Hungary (from the anthropological collection of the Natural History Museum of Budapest). The projection of the tuberculum minus disturbs the view. Approximate age 26–30 years.

Fig. 2 Roentgenogram of proximal hu from the Eneolithic period, Tiszapolgár, Hu (from the anthropological collection of the ral History Museum of Budapest). The p tion of the tuberculum minus disturbs the Approximate age 51–60 years.

anged, that of the diaphysis is more ival.

21–22 *years.* The epiphyseal line is npletely ossified. Here and there on the ernal surface traces of cartilage indi- e the last points of coalescence (fig. 4). e internal structure of the epiphysis is lially arranged, that of the diaphysis is the most part ogival.

'ig. 3 Proximal epiphysis of macerated hu- rus from a male, 18 years of age (contempor- cadaver). Epiphysis and diaphysis not yet ted.



'ig. 4 Proximal epiphysis of macerated hu- rus from a male, 21 years of age (contempor- cadaver). Remnant of epiphyseal closure in region of the tuberculum minus.

23–25 *years.* The development of the metaphysis is accomplished. The internal structure of the epiphysis is no longer quite radial, that of the diaphysis is ogival. The medullary cavity is far from the collum chirurgicum.

26–30 *years.* The radial arrangement of the internal structure of the epiphysis is fading. The internal structure of the diaphysis is ogival. The medullary cavity has not yet reached the collum chirurgicum.

31–40 *years.* The internal structure of the epiphysis has lost its earlier characteristic appearance. The internal structure of the diaphysis is more columniform. The most superior parts of the medullary cavity may approach the collum chirurgicum (fig. 5).

41–50 *years.* The columniform structure of the diaphysis is discontinuous. The cone of the medullary cavity has reached the collum chirurgicum. Between the cone

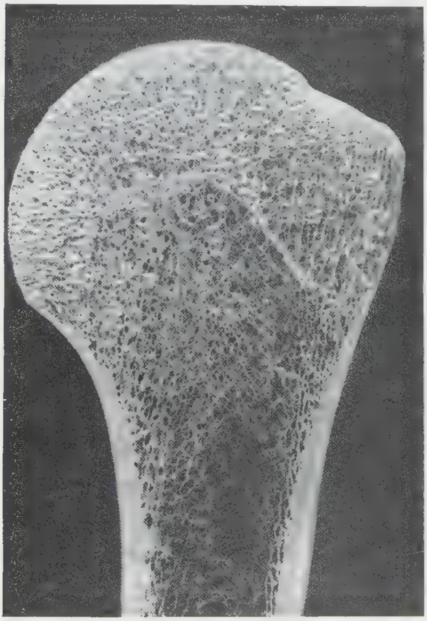


Fig. 5 Proximal epiphysis of macerated and sectioned humerus from a male, 35 years of age (contemporary cadaver). The internal structure of the epiphysis is no longer characteristic; that of the diaphysis is rearranged from pointed to columniform. The cone of the medullar cavity is approaching the collum chirurgicum.

and the epiphyseal line lacunae may be in evidence.

51–60 years. Pea-sized lacunae appear in the tuberculum majus.

61–74 years. The outer surface of the bone is rough and the cortex is thin. The diaphyseal structure lacks characteristic features. The medullary cavity has reached the epiphyseal line. Bean-sized, or even larger, lacunae are present in the tuberculum majus (fig. 6). X-ray pictures of the caput show increased transparency.

Over 75 years. The external surface of the bone is rough. The tuberculum majus has lost its prominence (fig. 7). The cortex is thin. Very little spongy tissue remains in the medullary cavity. In the gross specimen the epiphysis is very fragile. X-ray pictures of the caput show an increased transparency.

In evaluating the above age changes it is important to know whether the bones are male or female because the changes occur at different times in the two sexes. The difference, which favors the female, amounts to two years at puberty, 5 years

Fig. 7 Macerated proximal humerus fron female, 97 years of age (contemporary cadav The tuberculum majus is already atrophied hence scarcely protuberant.

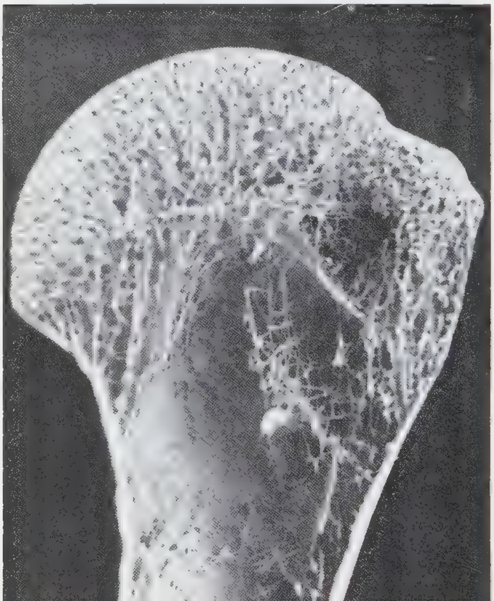


Fig. 6 Proximal epiphysis of macerated and sectioned humerus from a male, 64 years of age (contemporary cadaver). The medullary cavity reaches the metaphysis. There is an independent cavity in the tuberculum majus.

at maturity, and 7–10 years in seniu It should be noted too that Hansen at butes to a later period than I do the exp sion of the cone of the medullary cav and the consequent rarefaction. This accounted for by the fact that Hansen corded only the level of the cone of medullary cavity whereas I have add to this observation the rarefactions exte ing beyond the cone. However, it shou not be expected that the characterist enumerated above for each age level cur with literal exactness, especially in t middle-aged group. Nevertheless, such v iation, and especially the absence of c tain expected changes, do not dimini the value of the metamorphosis for p poses of age determination. Atypical cas are few, but, for example, minor lacun rarefactions do occur in the tuberculu majus at the age of 30 and, on the oth hand, they are not always in the me physis at the age of 70. According Bruno, the earliest appearance of ra factions is around age 40. In all su atypical cases other criteria will indic the true age. In work of this sort, course, the reliability of the age det minations depends mainly on the exp ence and practice of the observer. It he

so to make all of the observations and mparisons at one time.

Although this method of determining e from the humerus is intended pri- arily for use in connection with current oblems, the question arises as to the mains of ancient man. Obviously, in the tter case there is no way of checking on e reliability of the determinations. Also, course, chronological and physiologico- ological ages are not identical. This dif- rence may increase as we go back in ne, just as today it varies among peoples ing under different circumstances.

Finally, I should mention that Hansen als not only with humerus but also with e femur. Of the latter he examined 250 ses. Jacqueline and Veraguth ('54) also udied the internal structure of the femur, t in persons older than 60 years. Ac- rding to these studies the femur does not ow such distinctive age changes as does e humerus. Obviously, however, more likely to be learned by studying the two nes together than either one alone.

SUMMARY

The history of studies relating to age anges in the internal structure of the umerus is outlined. From these studies is assembled a list of characteristic changes to be found at successive age periods from 15–16 years to over 75 years.

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sion of Triquetral and Lunate Bones Shown Serial Radiographs

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he apparent fusion of triquetal and ite bones has only once been illustrated, ar as we know. Silverman ('55) gave e reproductions of radiographs of the hand of a negro child at the ages of and 8 years. At 6 years, the two bones n to be separate: at 7 years they over- and at 8 years, fusion is complete, a dense line at the distal edge of the bined bone, and no notch or groove ole at the place where union of bone urred. The radiographs were taken be- se the child had sickle cell anemia, and discovery of the fusion was accidental. ver the last 8 years, we have been owing the growth, and the bony de- pment, of boys at a large school for ican children not far from Kampala, we have found 5 instances of trique- -lunate fusion in the radiographs of children aged 6 to 16 years, an inci- ce of 2.1% : and we are reproducing iographs that show the fusion as a tinuous process. The 5 children were of the Bantu tribe, the Baganda, who abit that part of Uganda around Kam- a. They are a tribe showing much ad- xture (Oschinsky, '54): they are shorter stature, and less dark of skin, than the otic tribes of Uganda, and shorter of ture and stockier but usually darker skin, than the tribes usually known as mitic.

The radiographs were all taken with a tance between anode and film of 91.5 (36 in.). "Ilfex" non-screen film was d, in cardboard exposure holders. The rent was 60 ma at 43 kv and the time exposure 0.6 to 0.8 second.

RESULTS

Figures 1 to 3 illustrate various phases the fusion completed to approximately the same extent at chronological ages of 11 years and two months (fig. 1, c, 11 years, three months (fig. 2) and 11 years and 7 months (fig. 3, c). In figure 4, the fusion is not so advanced even at the age of 17 years, one month. The age of development of the whole hand (the "bone age") according to the standards of Greulich and Pyle ('50) is given with each chronological age. The bone ages corresponding to the chronological ages just mentioned are 10 years, 6 months (for figs. 1, c and fig. 2); 11 years, 7 months (for fig. 3, c) and 15 years (for fig. 4, f).

The figures show two points of special interest. The triquetral portion is more elongated and waisted than it is in the normal American boy and the outline of the lunate shows that there must be considerable rotation of the joined bones about an arcuate axis more or less parallel to the radio-ulnar joint. The rotation shows most clearly in the 3 pictures in figure 3, but it can also be traced in figures 1 and 4. We are satisfied that the changes of outline are not artefacts due to faulty positioning of the hands, but must represent a true rotation.

Although the figures show only the left hand of each child, the right hands were also examined radiologically, and all showed fusion. All the 4 children were right-handed.

The coarse trabeculation of the bone that shows in all the photographs is an African characteristic for which we have at the moment no explanation. One child (the one whose hand appears on fig. 2) had the sickle cell trait, but did not have sickle cell anemia.

Our fifth example of fusion, which is not illustrated here, shows fusion approximately the same as in figure 1, d, at a

chronological age of 15 years 2 months and a bone age of 14 years.

DISCUSSION

Summaries of the appropriate literature can be read in Smitham ('48) and Minnaar ('52). Triquetral-lunate fusion seems to be more common in negroes than in white people, and most of the reported cases are in the right hand; it is not certain, however, to what extent this is because only the right hand was examined in many of the subjects. It may be present in more than one member of the same family and it is not associated with comparable abnormalities of the feet. The largest series of negroes in whom it has been sought is that of Smitham ('48) who found it in 37 of 600 adults (6.2%) and in three of 80 children (3.8%). Obviously it may not have been complete in some of the children when they were examined. The adults and the children were of mixed tribes thought to be mostly Nilotic in origin. It is often bilateral, and Minnaar ('52) showed it in three forms: as incomplete, but with close apposition of the adjacent surfaces, resembling a pseudo-arthrosis; as a fusion with a notch at the join on the distal side, and as a fusion with no mark of its origin. The fusion was bilateral in 4 out of the 5 of our children: the fifth child had left school when we were preparing this paper, and could not be examined again. Our examples show Minnaar's three forms, but we cannot say if they represent the final stages of the fusion. It is probable that in most cases, the fusion proceeds until the line of fusion is obliterated, but our figure 4 may possibly indicate the formation of a pseudo-arthrosis. We have a series of radiographs of the hand of the brother of the child shown in figure 2, but he does not have the fusion.

The elongation of the triquetral bone to which we have drawn attention is not usually found in African children, but seems to be related to the fusion. Drawings of a fused bone, and of normally separate bones, are given by McConnell ('07) and the fused triquetral part is much more elongated than the separate triquetral. The same elongation of the triquetral element is shown in the hand of a man described by Curr ('46–47): in his c
example, in a woman, the shape is r
mal, but it is elongated in Silverma
('55) case.

Curr ('46–'47) and Smitham ('48) s
that the function of the wrist is not
fected by the fusion. We decided to co
pare the function in our 4 available
dren with that of 4 other children wh
triquetral and lunate bones were not fus
who were of the same chronological a
and approximately the same bone age, a
who were all right-handed. Although
knew that in some movements of the ha
the normally separate triquetral and lun
bones move as one, we expected to
limitation that could be related to the f
sion. We measured first dorsiflex
starting with the arm and hand flat on
angle board, and forcibly flexing the ha
until the wrist began to lift off the boar
the angle between the palmar surface
the board was then recorded. There
no consistent difference of the angle b
tween the two groups of children, and t
x-ray appearances of the bones in full d
siflexion were essentially the same in b
groups. Palmar flexion was not measur
because it was difficult to devise a sat
factory test that could be followed ra
logically. The deviation of the radius a
ulna on the carpus was estimated with
arm and hand flat, and the hand h
firmly in place. The arm was then mo
from side to side without any rise fr
the board, to the limits of deviation. T
limits were much easier to establish th
the limits of flexion. Radiographs
peared to show greater deviation in
children with the fused bones than in
other children, and this impression was
the whole confirmed by measurements.
all the hands had been positioned in
actly the same way, and as the taking
the radiographs was standardized, the fi
of each "fused" child could be placed
that of his "control" so that the outli
of the second and third metacarpals of
two hands coincided, to see how far
radius and ulna had moved. It was a
possible to draw lines through the lo
axes of the second metacarpal and
radius, and to project these lines a
measure the angle they enclosed. The
sults of inspection and measureme

reed: deviation to the radial side was eater in all the 4 "fused" children than the controls, and deviation to the ulna le was greater in three of the 4. The ild who was the exception is that whose nd is shown in figure 4. He was the lest of the "fused" children, and it is ssible that the extent of deviation in ch children bears some relation to age. e intend to examine this possibility when her examples of fusion are found in der children or in adults.

Various suggestions have been made to plain how the fusion occurs. The most ausible is that one mass of cartilage presents the two bones, without the normal joint space and synovial membranes tween them, and that ossification begins om two centers, in the way commonly en in other bones, such as the epiphysis the head of the ulna (see fig. 4, a). oof is unlikely to be obtainable by biopsy at autopsy, and the best method seems be section of unossified cartilage of children who are still-born or die at birth, and e demonstration of an absence of mesorm differentiated for the normal joint. Minnaar ('52) thought that the fusion ight be an indication of primitivity. The ylogenetic evidence seems to be against m (Wood Jones, '49). The proximal row carpal bones probably represent the imitive radiale, intermedium and ulnare, nich are not fused. If we wanted to find avistic characteristics in the hand of the egro, we would look for an os centrale, nich is a separate bone in *Tarsius spectum* and even in the orang utan, or for o bones under the bases of the 4th and h metacarpals, which are represented by single bone in all living mammals. The Negro has neither the one bone nor the two.

SUMMARY

Five examples of triquetral-lunate fusion have been found in serial radiographs of the hands of Bantu children, and the process of fusion is illustrated.

The triquetral part of the conjoined bone is usually more elongated than a separate triquetral bone.

In young children with the fused bones, the extent of deviation of the radius and ulna on the carpal bones may be greater than it is in children of the same age in whom the bones are not fused.

The fusion is probably the result of ossification from two centers in a single mass of cartilage. It is not a primitive characteristic.

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PLATE 1

EXPLANATION OF FIGURES

1 a Chronological age 8 years, 9 months; bone age (see text) 7 years, 6 months. Triquetral and lunate parts separate. The triquetral is very elongated.

1 b C. A., 10 yr. 2 mos., B. A. 9 yr. 3 mos. Joint line for hamate and capitate established, but apparently discontinuous.

1 c C.A. 11 yr. 2 mos., B.A. 10 yr. 6 mos. Fusion now complete, with only a slight indentation on the proximal border at the place of fusion.

1 d C.A. 12 yr. 2 mos., B.A. 12 yr. Inferior surface now completely smooth. The bone is more rotated (on an axis parallel to the radio-ulnar joint) than in (c) and the surface for articulation with the capitate shows as a large wing.


1b
1d

PLATE 2

EXPLANATION OF FIGURES

2 C.A. 11 yr. 3 mos., B.A. 10 yr. 6 mos. Fusion complete, but line of fusion just visible and proximal surface indented. Rotation less than in figures 1, d and 3, c. The triquetral portion seems to be very elongated.

3 a C.A. 9 yr. 7 mos., B.A. 10 yr. The elongated triquetral appears to be touching the lunate.

3 b C.A. 10 yr. 7 mos., B.A. 10 yr. 7 mos. The bones have reached the stage of fusion shown in figure 1, b, but the joint line for hamate and capitate cannot be clearly seen.

3 c C.A. 11 yr. 7 mos., B.A. 11 yr. 7 mos. Fusion corresponds to that in figure 1, d but the line of fusion is still visible and the proximal surface is slightly indented. The rotation is slightly more than in figure 1, d.


3a
3c

PLATE 3

EXPLANATION OF FIGURES

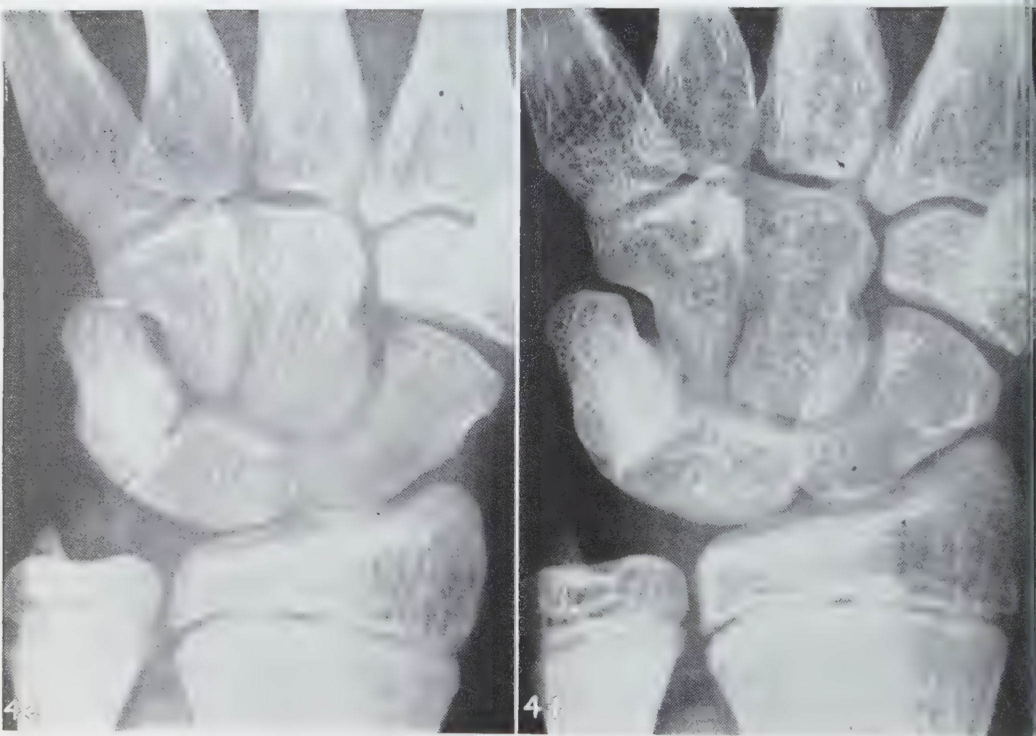
4 a C.A. 10 yr. 4 mos., B.A. 8 yr. 6 mos. The triquetral has a normal outline except for a slightly protruding corner on the proximal surface.

4 b C.A. 12 yr. 11 mos., B.A. 10 yr. 6 mos. The elongation of triquetral is made more obvious by an extension of the protruding corner. The joint line for hamate and capitate can be traced on triquetral and lunate.

4 c C.A. 13 yr. 7 mos., B.A. 11 yr. 3 mos. The bones are almost touching.

4 d C.A. 15 yr., B.A. 12 yr. 6 mos. Fusion appears to have taken place in the mid-parts of the opposed surfaces, but there are deep notches distally and proximally.


4a
4b
4c
4



4 e C.A. 16 yr. 1 mo., B.A. 13 yr. 9 mos. Fusion is more complete, but the deep notches persist.

4 f C.A. 17 yr. 1 mo., B.A. 15 yr. The line of fusion, although partly obscured by the pisiform, can still be traced, and there is a small proximal notch and a large distal one. The surface for articulation with the ulna and radius is smooth. The rotation is approximately the same as in figure 3, c.

ne Anthropometry of the Manual Work Space r the Seated Subject[1]

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This paper is an exploration of the ace-geometry of hand motions as they ate to young men in the seated posture. is primarily a presentation in functional thropometry, but the information de- ed should have practical use in improv- g the design of work areas. The pilot of airplane, the driver of an automobile, assembly worker or the machine oper- r all perform critical tasks with their nds. Controls and switches or objects on which work is to be done must not erely be within reach, they should also placed in the best possible spatial posi- n relative to the operator. This ideal sition has not yet been prescribed.

A detailed job analysis of a specific man- l operation should of course improve the rk area materially, but this information s little transfer value to another situa- n. Our work is concerned with the gen- al range of hand motion, and we have empted to find principles applicable to work situations involving the seated sition.

The approach is anthropometric—but in entirely different sense from traditional thropometry. Our measurements of the ace within reach of the seated subject r all possible upper limb postures repre- nt an approach to a dynamic anthro- metry. The method of measurement is direct, and it involves a certain novelty anthropometric procedure; this shows especially in the methods of gathering w data, of making measurements, and treating data.

A study of the functional-anatomical ckground for limb motion paralleled this udy. Relevant work (Dempster, '55a, 5b, '56) involved a study of the motions the major limb joints and a clarification the characteristics of the *link* mechanisms involved. (A link is the straight line or core line through a body segment between adjacent joint hinge points; it is the mechanical unit of body motion.) Older sources that cannot be ignored in a functional-anatomical-anthropometric study of this type are: Fischer ('07), Fick ('11), Strasser ('17), Braus ('21), Lanz and Wachsmuth ('35), and Mollier ('38). The Albert-Strasser globographic technique (Albert, 1876; Dempster, '56) for demonstrating the range of individual joint movement has provided useful background material. Equivalent work on living subjects is not available. Joint range studies on living subjects are typified by papers by Gilliland ('21), Sinelnikoff and Grigorowitsch ('31), Glanville and Kreezer ('37), Dempster ('55a) and Barter, Emanuel and Truett ('57). These studies are rather incomplete for certain joints and are not wholly satisfactory. Further work relating to age, sex, race, and occupation is warranted.

During the past decade or so, various authors have touched on aspects of the work place. Motion and time study workers (Barnes, '49; Branson, '52), psychologists (Chapanis, Garner and Morgan, '49; Hick and Bates, '50; McFarland, '53), engineers (Wallichs and Hulverscheidt, '35; Davis, '49; MacNeil, '54), and physiologists (Taylor and Blaschke, '51) have directed attention to spatial aspects of hand action. Dynamometric studies on hand forces by Hugh-Jones ('45) and by Darcus

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('51), Salter and Darcus ('52), Darcus and Salter ('53), Gaughran and Dempster ('55), Whitney ('58), and Dempster ('58) are relevant also. Randall, Damon et al. ('46) and especially King, Morrow and Vollmer ('47), King ('48, '52), McFarland et al. ('53) and McFarland, Damon and Stout ('55, '58) have considered dimensional problems of the seated subject. Commonly these references relate to empirical studies designed to meet specific problems of military and industrial personnel.

Orientation

If a part of the body such as the feet or buttocks is placed motionless on a supporting surface, the relative range of motion of some more mobile part, as the hand, may be defined in terms of a space geometry related to the immovable region. In effect, the body can be regarded as if it were within a three-dimensional Cartesian coordinate system which has its origin at a point on the supporting surface; the potential motion of any moving point—for instance some point on the hand—may be located within a region or space envelope with boundaries that may be scaled off relative to the x, y, and z coordinates. In the present study, the subjects were always seated. The envelope has a specific size, shape, and relation to the seat, trunk and legs; like the atom or solar system, however, it is bounded by an intangible surface which in this instance represents the extreme range of motion of the reference point of the hand in different directions. The space itself is merely the region of potential position of the hand point. In order to visualize the space envelope and its modifications for different conditions, both the seat and the hand reference points must be clearly identified.

For the seated subject the most stable body region is that part touching the seat. In our procedures the subject's head lay in contact with a dental head rest, the back was against the wooden seat back, the buttocks were well back on the seat, and the thighs were directed forward; thus the trunk was relatively stable for all hand positions. We have selected the midsagittal point of the junction of the seat and back as a reference ("R") point. This, in effect, is the zero point on an x, y coordinate system, to which are rela[ted] the variable distance and angulation [of] the hand point as it travels in its outerm[ost] range over the surface of the space [en]velope.

The hand is a complex anatomical str[uc]ture; if a part of it is to be a referen[ce] point, a precise posture must be assum[ed]. Our approach starts with the recognit[ion] that the hand in a position of rest refle[cts] a balanced system of minimal forces. T[his] is a sort of mean hand posture from wh[ich] other postures, including those involvi[ng] finger activities, are deviations. Of cour[se] there is no one rest position; it varies w[ith] how the hand rests with relation to t[he] forearm and with the degrees of wr[ist] flexion or extension. When, however, t[he] hand and forearm lie passively and supi[ne] on a horizontal support with the wr[ist] straight, the rest position is fairly avera[ge]. This rest posture is approximately t[he] same as when the hand lightly grips [a] cylindrical rod of about 30 mm (1 1/8") diameter. In our work the gripping of [a] standard rod proved an easy way of getti[ng] the hand to assume a position compara[ble] to the mean rest posture. Now, when t[he] hand gripped such a rod and the hand a[nd] forearm hung inert and vertically, the g[rip] angle for 40 men relative to the long a[xis] of the forearm was found to be 102° ± [?] (obtuse angle on the radial side). (T[he] grip axis was also about 14° more supi[ne] than a line between the radial and ul[nar] styloids in the semi-prone position [Dem[p]ster, '55a].) The grip angulation increas[es] as rods of notably larger diameters we[re] grasped, but it was little changed for [ob]jects down to the size of a pencil.

In this study the axis of the grip w[as] regarded as the core line of a 30 mm r[od] held in the hand. The thumb, or rad[ial] end of the rod, was used as a pole of ref[er]ence. A point on the axis of the rod at t[he] level of the third finger was arbitrar[ily] taken as the hand point or grip center [–] hereafter called "grip point."

It is the outermost range of this gr[ip] point which, according to our usage, co[n]stitutes the surface of the space envelo[pe]. At the surface of the space envelope [as] defined by the grip point, the fingers [or] any other part of the hand may momenta[rily]

lie exterior to the grip point and to this ent they will project outside of the ace envelope; similarly, the subject's dy, and parts of the arm in certain positions, lies outside. Since the position of t of the hand is a generalized mean sture, the space envelope for the index ger tip of the pointing hand, or for the nch position of the fingers, can be deed by adding appropriate dimensions the front surface of the space envelope the resting hand (and subtracting from rear surface).

The hand mass of the seated subject y be moved in either of two ways; it n move by *rotation* or by *translation*. In *ational* or angular movement, the hand y be turned or twisted so that the angle the grip axis is changed relative to the rtesian system (or the floor or walls of a m). In *translational* movements, howr, the grip angle remains constant; the nd in translational movement may be ved in a straight or curved line in any ection, but there is no angular change the grip axis relative to the room. The nd may move through three degrees of edom for translational movement—up d down, right and left, forward and ckward. It may also move through three ditional degrees of rotational freedom—ation in the sagittal plane, rotation in oronal plane, or rotation in a transverse ne; but it has only these 6 degrees of edom for potential movements. In our proach, translational movements of the nd, it will be seen, will receive primary ention.

When the hand, as the end member of chain of extremity links, is kept in a nstant angular orientation relative to a ed "R" point, movements at the wrist, ow and shoulder permit an extensive nge of translational hand movement. e space envelope enclosing the total nge of such translational movements s a distinctive shape, which results from unique combination of both the range d freedom of joint rotation by all of the per limb joints and the limitation imsed by the constant orientation of the nd. The relative dimensions of the limb gments in different people, of course, o have a determinant relation to the ape but this effect is small.

We employ the term *kinetosphere*, from *kineto*, movement, plus *sphere*, region of, as an aid in analyzing the work area. The term applies to the total range of translational movement of the end member of a series of links relative to an "R" point; moreover it applies only to the arbitrary situation in which the end member is continually maintained in a constant angular orientation relative to a system of reference coordinates. In this study the hand was always directed straight forward; other kinetospheres could be defined for study with the hand pointing up, to the left, or down.

One should appreciate the nominal character of the kinetosphere. It is not merely another word for the work area but a concept which defines the space-shape which encloses a specific class of hand motion, translational movement only, so that it can be analyzed. The dimensions of such an envelope may be measured, and its shape may be reconstructed. The boundary outlines of sections through the kinetospheres can be grouped and compared, and similar kinetospheres from different individuals can be combined and averaged. The variability from subject to subject can be treated statistically. But kinetospheres have no existence apart from a rigidly imposed set of conditions, which limit the hand to purely translatory types of motion. The value of the concept is both in its use as an analytical tool for exploring body motion and in its ability for defining the space requirements for types of hand motion. The designer of planned work areas should thus be aided practically.

Each arbitrary hand orientation has only one kinetosphere. When a group of kinetospheres representing a related series of hand orientations, i.e., different classes of grip rotation for the same direction of hand pointing (viz., forward), are added to one another, we call the cumulative pattern a *strophosphere* from *strophe*, a turning or twisting, plus *sphere*, region of. The related series of hand grip orientations may represent a series of discrete wrist tilts in the sagittal plane (relative to the room); the series may involve a prone to supine twist about an anteroposterior hand axis (again relative to the room), or a wrist movement may be con-

cerned with side-to-side hand postures about a vertical axis. The term applies to the space envelope, which permits three degrees of translational freedom for the hand plus one degree of rotational freedom relative to fixed coordinates. (Other strophospheres, not studied, can be visualized—the hand and forearm pointing up, in, out, or down, in each instance including a systematic grouping of rotational motions.) When one or two additional degrees of rotational freedom are included, the complexity increases, since the sequence of adding involves 6 possibilities of combinations; thus the value of the analysis breaks down.

Through kinetospheres and strophospheres, however, one may dissect the work area in terms of the hand positions which are possible in different regions of the total space within reach.

A more extensive term *ergosphere*, from *ergo*, work, plus *sphere*, region of, or work area, may apply to the total range of possible hand positions relative to an "R" point; we would apply the term ergosphere to the hand space representing wholly unrestricted movement for any and all hand and forearm orientations—the only condition would be that the subject's back and buttocks had the constant relationship to the "R" point.

METHODS

Twenty-two male college students (ages 17–33) formed the study sample. In build they ranged from median to muscular; rotund and thin types were excluded. The more significant mean dimensions were: stature—175.7 ± 4.5 cm (69.4 in.); sitting height—91.5 ± 3.2 cm (36.1 in.); acromial height (sitting)—61.3 ± 3.2 cm (24.2 in.); and upper limb length (acromion to dactylion III—arm straight, horizontal, and forward)—72.8 ± 2.9 cm (28.7 in.).

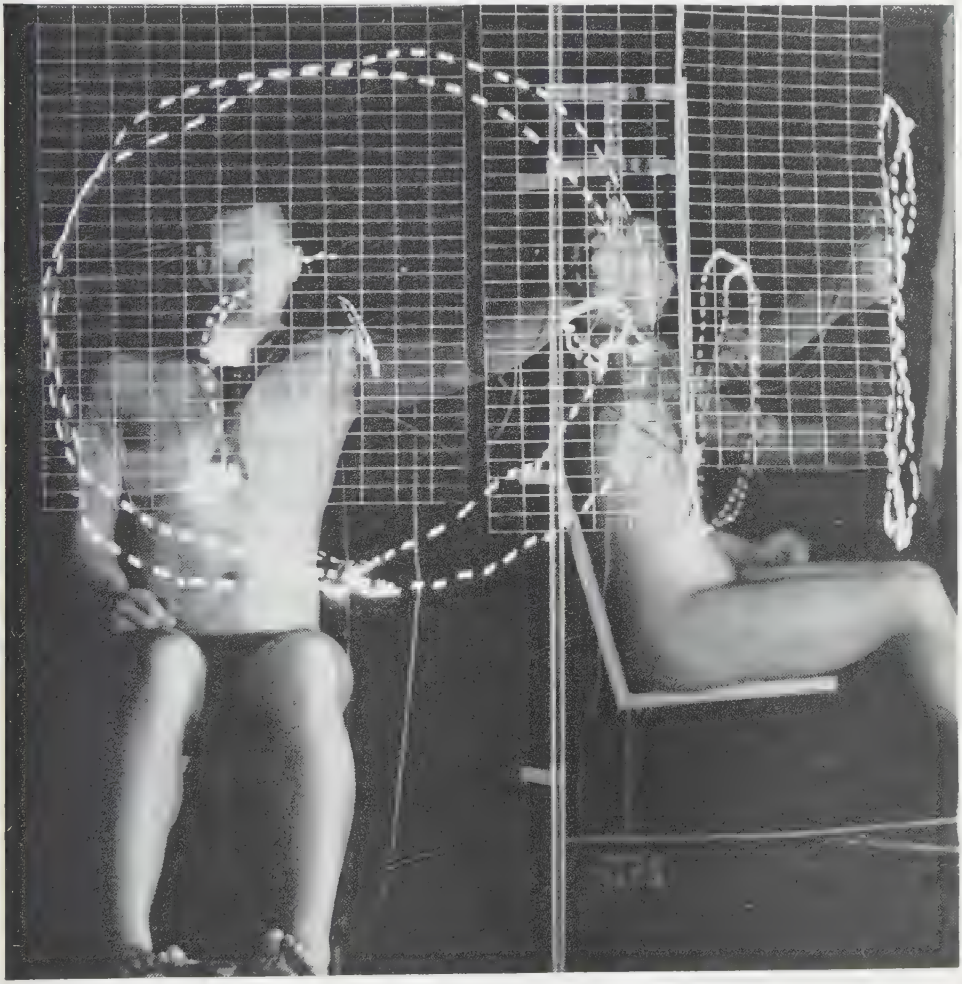
Our primary records (fig. 1) were a series of photographic negatives—time exposures in the dark—which showed the path of movement of a small light at the hand (i.e., over the "grip point") as it was moved by the subject. The subject sat facing the camera in a special seat and, for the first record, he moved his hand over a wire screen at arm's length so that it described a circuit at the extreme limit of movement. In his hand he held an appliance consisting of a screen grid and an adjustable hand grip (referred to later) which assured that the grip axis was maintained in some standard orientation throughout the circuit. Then the seat and subject were advanced a measured distance relative to the plane of the screen and a new hand circuit was photographed. The subject was moved forward progressively in this step-wise fashion and additional hand circuits were recorded for each position of the seat and subject until each level of the whole kinetosphere had been photographed. The photographic records provided a group of equally spaced frontal serial sections through the kinetosphere. From these, a variety of data could be derived, including three-dimensional models.

The seat on which the subject sat was of wood, and it had a back and a headrest. The basic plan was that of the Air Force fighter cockpit of the early 1950's. The seat was 15 in. deep and 11 in. wide; because of the narrow seat back, the subject's elbows and shoulders were unimpeded, thus the posterior range of the grip point was not artificially reduced. The seat was tilted 6° to the horizontal. The back was 26 in. high, and it tilted back 17° from the vertical. At the top of the seat back, an adjustable dental headrest was mounted. The position of the foot rest and foot platform relative to the seat could be adjusted by oblique upward and forward movements as in the airplane cockpit, so that individuals of different heights could be accomodated comfortably. Through adjustments of the height of the foot platform, the vertical distance between eye level and heel was made a standard 39.5 in. for each subject.

As shown in figure 1, several wire grids (1 × 2 in. mesh) were suspended from an overhead horizontal bar parallel to the picture plane of the camera to provide a frontal reference plane behind which the hand could move. A large 5 × 7 ft. mirror set at 45°—on the subject's left—showed a side view of the grid, subject and seat.

The hand appliance (fig. 2), which was constructed for the left hand only, co

ed of a handle—a 30 mm aluminum —and a small rectangular orientation l. Scotch-lite reflective tape was added he vertical midline and the horizontal ders of the grid to enhance visibility he photographs. Dental moulding comnd was shaped about the aluminum to provide a good fit for the thumb, n and fingers of the left hand; thus handle could be grasped in only one . An aluminum ball at the thumb end he grip had a series of threaded taps which the small rectangular grid could be attached at one or another of a number of selected angulations relative to the hand grip. When the grip was held firmly in the subject's left hand and the forearm, wrist and grip were aimed straight ahead, with the grip vertical, the grid was initially set upright in the frontal plane (i.e., 0°). After this initial adjustment, 7 other grid positions (fig. 2) were obtained by screwing the grid to the ball at other standard angulations. In each position the grid and the grip were oriented at a specific angulation to one another. When the grid



ig. 1 Method for recording extreme movements of the "grip point" of the hand in the plane of wire screens. The figure at the right is a 45 mirror image of the subject shown front view. During a time exposure a flashing light at the level of the grip point marks out a path of movement. The d grid assures a vertical hand grip orientation. Fixed reference lights lie over the sternum; other ing lights are attached to the shoulder and elbow.

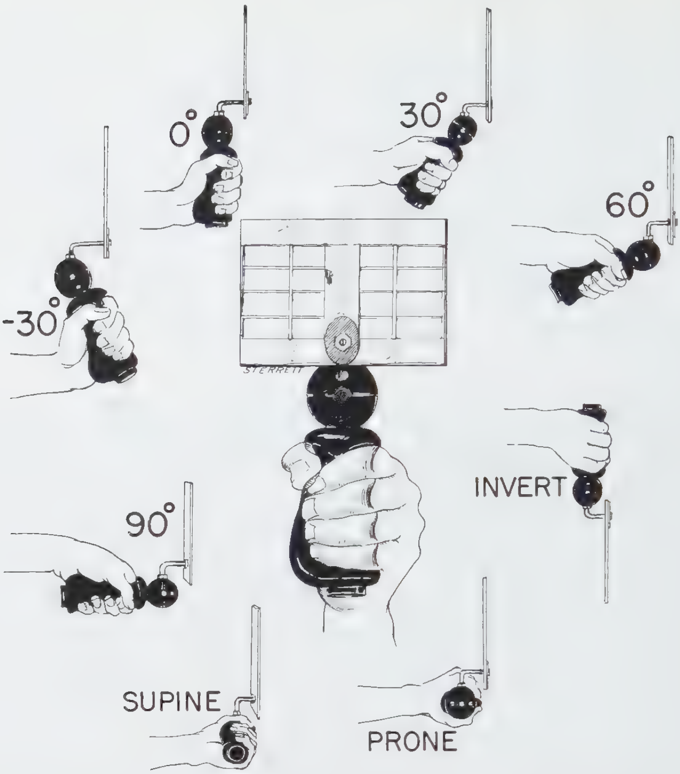


Fig. 2 Hand grip and reference grid designed to keep the hand in a fixed orientation while h
movements were recorded. The 8 standard hand orientations studied are illustrated.

was held upright in the frontal plane (for instance, behind and parallel to the hanging grids of figure 1), the hand grip axis of necessity assumed some fixed angulation to the vertical. Five grip orientations in the sagittal plane (relative to the room) were permitted and these were: 30° back (i.e., −30°; upper end of the grip directed backward and upward), 0° vertical, 30° forward, 60° forward and 90° forward (i.e., the grip was horizontal and directed forward). In adidtion to the 0° position, three other positions in the coronal plane were permitted by the ball at the hand grip. These were the prone and supine positions and a vertical position with the thumb downward—the invert or 180° position.

A 1/25 watt neon glow lamp was adjusted to the hand grid, so that its position in photographic records lay at or near the center of the grip, i.e., the "grip point." Sometimes other lamps also were fitted over the shoulder and elbow joints.
flashing rate of 6 per second, controll
by an electronic system, allowed easy
ferentiation of traces when more than
appeared on the film. A Graflex camera
15 ft. distance from the reference pla
of the suspended wire grids included a fi
like figure 1. A red lens-filter transpar
to neon light was fitted to the camera, a
a low-intensity blue light that did not
cord through the filter was used for g
eral illumination of the otherwise da
ened room. Dark backgrounds were p
vided for both the direct and mirror-ima
views.

For the record-taking, the subject
squarely against the seat back and he
rest, and he directed his arm straight f
ward with the shoulder protruded and
grid of the hand grip held behind and p
allel to the suspended reference gri
While the arm was in this position,
seat was moved forward or back until

ance between the grid plane and the point of the seat was as short as pose—a three-inch or less clearance was nitted for the movements of the hand ›. The actual seat-to-grid distance was ısured and recorded. When this adment was made, the reference grid at hand was 3 in. or closer to the zero s.

'he first photo record was taken with neon lights flashing as the subject ly moved his hand clockwise in the ıtal plane—then counterclockwise—ugh the widest possible complete cir-. The hand grid was to be kept conıtly in its upright orientation just be-l the reference grid; this was critical e a constant grip orientation was es-ial if the hand motion were to be ctly translational. In the faint blue t of the room, the camera operator d see both the direct and mirror-view he subject; the mirror-view showed the rence grid edge-on, and any deviations n the frontal plane could be seen. Any wise tilting of the grid could be seen ctly. If any significant deviations were ı, the camera operator could direct the ect to repeat the record. After prac-runs in both the clockwise and count-ockwise directions, the camera was ıed and the path of both circuits of neon lamp was recorded. At some time ng the movement, a speed-lamp (= be) flash was set off to illuminate the le view including an instantaneous ge of both the direct and side views of subject (fig. 1).

/hen a new film (super XX, film pack) in place for a second exposure, the and subject were moved a fixed stand-distance (three or 6 in.) closer to the rence grid, and a new pattern of hand ement was photographed. After each osure, the seat and subject were ad-ced by the standard distance until the ect no longer had space to move his d between the reference grids and his 7. One or another panel of the grid ront of the subject was then raised or, ey touched him, removed. Movements he hand at the side of or behind the 7 were traced over a single grid at the of the body.

Since the records were intended to show the range of hand motion, it was important that adventitious trunk movements did not augment the motion. Figure 1 shows a yoke of sheet lead lying on the sternum with flashing neon lights over the manubrium and xyphoid. Where the photo negatives showed that the lights had moved as much as 1.5 in. during the clockwise and counterclockwise movements of the hand, the record was later repeated.

The photo negatives for each subject-grid distance were projected in an enlarger to exactly 1/5 natural size. Tracings of each negative were made on paper separately, including neon light paths as well as orienting landmarks and dimension marks in the background. Next, as a separate operation, a mean circuit was drawn in between the tracings of the clockwise and counterclockwise circuits of the neon light; this mean circuit was thereafter taken arbitrarily as the definitive record of "extreme" hand movement in the plane of reference.

Planimeter measurements of the area of each mean circuit were then made from the tracings. These areas were next plotted as ordinates on graph paper (fig. 5) with a spacing along the abscissa comparable to the distance between sections; the location of the "R" point and reference grid was also drawn on the graph. Two corrections were necessary before the graph was strictly accurate; first, the mean antero-posterior distance between the hand light and the reference grids (as seen side view, fig. 1) had to be measured; secondly, the distance between the light (or reference grid) and the grip point—different for each grip orientation—had to be added. After these corrections had been plotted relative to the reference grid position, the plot was properly related to the grip point. An accurate area-to-distance curve could now be constructed (fig. 5). The area under the curve, as measured by planimeter, corresponded (at one-fifth scale) to the volume of the kinetosphere.

In addition, through a treatment of moments along an antero-posterior axis (i.e., areas of sections x distances from a zero point) the fore-to-back distance of the centroid, or center of gravity, of the kineto-

sphere could be calculated and located relative to the grid plane and to the "R" point of the seat.

Next through the suspension of cardboard cutouts, the locations of the centers of gravity were found for two sections—that just directly ahead of and that immediately behind the kinetosphere centroid. The centers of gravity of the two sections were located relative to a vertical coordinate corresponding to the mid-sagittal plane of the subject and a standard transverse coordinate near the shoulder level; then tracings of the two sections were superimposed and, by appropriate "weighting," a new "mean" section contour with its center of gravity was drawn in for the correct antero-posterior distance of the kinetosphere centroid. We assumed that this section-centroid would have vertical and horizontal coordinates comparable to those of the whole kinetosphere. With this approximation, it became possible to relocate the centroid of the whole kinetosphere relative to the "R" point of the seat—anteriorly, laterally, and vertically.

A convenient way of comparing kinetospheres involved the use of sagittal, frontal, and horizontal sections through the centroid. This required a reconstruction of contours from measurements derived from the sections. The technique involved first the marking of the horizontal fore-and-aft projection of the centroid of a kinetosphere upon each tracing in a series of sections. Then, at points directly above and below the centroid on each section, the distances to the section outline were measured. These measurements were next plotted as ordinates on graph paper (above and below a horizontal line indicating centroid level); the horizontal spacing was comparable to that between sections. When the points were connected, the plot represented a sagittal section through a kinetosphere at centroid level. The "R" point, kinetosphere centroid, and other points were added also. Comparable plots showing transverse measurements at centroid level permitted the development of a horizontal section through the kinetosphere. A coronal section through centroid level was determined, as mentioned above (previous paragraph), by a "weighting" of the contours of two section outs—the ones just anterior to and pos rior to the centroid.

The three sections cutting the kin sphere in mutually perpendicular pla that intersected the centroid could be terpreted as easily as three-dimensio plastic reconstructions; the shapes co be compared, by superimposing sec outlines; the contours could be supe posed and summated to give general patterns for a group of individuals, or t could be grouped to show strophosph patterns.

Actual three-dimensional reconstructi were made from tracings through re sentative kinetospheres. Much like wax plate reconstructions of embryologi these models were made from slices styrofoam plastic (12 × 12 × 0.6 or 1 in.); the thicknesses of the plates of fo plastic were just 1/5 of the three or 6 distance that the subject was moved tween records.

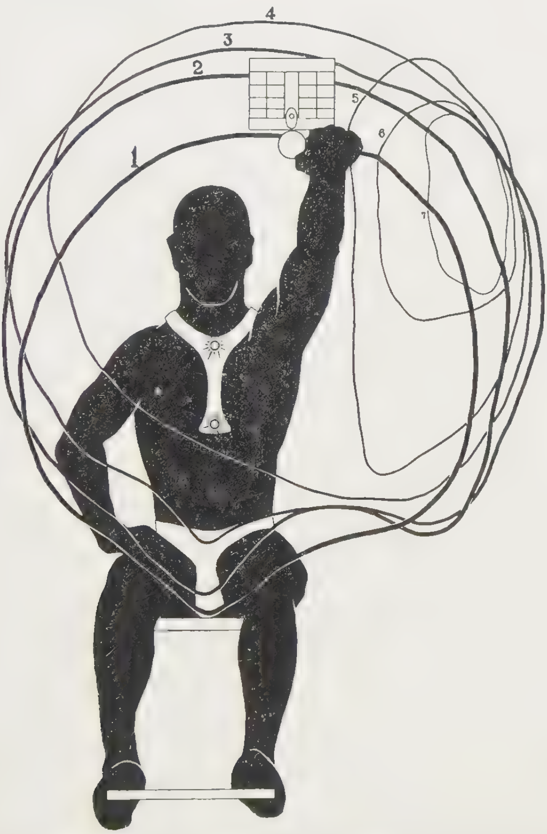
In the initial photography, each of 22 subjects went through the procedu 8 times; each time represented a diffe hand orientation and hence a diffe kinetosphere. From each group of rec (i.e., one kinetosphere for one subje we had as working data: (1) a grou 7 or 8 (or more) frontal tracings of m hand range having a known antero-p rior spacing, (2) plots representing sa tal, frontal and transverse sections thro the kinetosphere at centroid level, and area and volume data based on planir ric measurements.

Since the data relating to a single dividual were of limited practical in est, our data were typically summate averaged in some way. For numer data, such as planimeter measurement sections, kinetosphere volumes, and tances, individual records were simply eraged. Where shapes were involved, c posite mean section contours were ne sary. The sagittal, horizontal, or fro plots (through a centroid) of different dividuals, as mentioned above, were su imposed relative to the seat coordin (and other landmarks in the original tographs) and traced in different col to avoid confusion, on tracing paper o translucent plastic; centroid locati

e indicated also. The mean centroid ation for all of the similar kinetospheres ether could be found through a con- eration of their moments. After this nt had been located, 8–10 lines were wn radiating out from the common cen- d to the contours of the superimposed ored tracings. Along each of the radi- ng lines, measurements were made of distance from the centroid to each of intersecting contours. These distances e then averaged to give a mean dis- ce, and this was marked as a point on radiating line. A mean contour could n be drawn through the points. In ad- on to the average contour, the distances he individual contours from the aver- were measured along the radii, and mean deviation was calculated. It uld be noted that the plus and minus mean deviation rather than standard deviation has been used as a simple measure to compare the variability of one region of the space-shape with another; M.D. = $\Sigma(D/n)$.

In gathering and processing the data, utmost attention was paid to obtaining correct orientations and dimensions. For this reason, the results obtained from the material at one-fifth scale could be projected back to natural size with no appreciable loss of accuracy.

All our records were taken from the left hand. Since the two hands should have about the same range of movement, the mirror image is roughly comparable to a direct record. Thus, when right-hand kinetospheres are implied, they are simply mirror images.



. 3 Seven contour outlines show the range of movement of the prone hand over a series of al planes spaced at 6-inch intervals. The relative position of the seat and subject are shown also; ghts attached to the yoke over the sternum indicated whether or not trunk movement contributed nd range.

RESULTS

Section contours and kinetosphere shapes

Since the basic data for this study consisted of a group of mean tracings of frontal-plane serial sections through each of the 8 kinetospheres of 22 different men, the general character and implications of the sections themselves must be appreciated. The sections illustrated (fig. 3) represent the range of motion of the grip joint of the prone hand directed forward for one of our subjects.

Superimposition of sections

The sections were superimposed relative to both the midline of the seat and a transverse line (near shoulder level) through a landmark at camera height in the background of the original photo. One sees a series of 7 rounded or irregular closed outlines which varied in size and orientation relative to the subject's body. The contours in this instance represented sections at a 6-inch spacing through the kinetosphere. The first section, that farthest forward from the body, was ordinarily roughly circular. If the subject could scarcely reach the grid, the diameter was small; in a larger contour, the first section could, as shown, have an irregular lower boundary over the knees. The limits of forward movement for the maximally protruded shoulder were determined by the fact that the hand, because of the obliquity of the arm in a wider circuit, would move away from the plane of the hanging reference grids.

As the subject-to-grid distance was shortened, the size of the circuits increased—particularly in the upper range. As the seat-grid distance was further reduced, ligamentous restraints to wrist abduction on the test-limb side and limits to adduction on the far side defined medial and lateral boundaries for movements of the prone hand. At the same time, a lower limit was imposed by contact with the knees or thighs. An upper limit was determined by maximum shoulder elevation and by the tendency of the raised limb to retract from the grid plane. The limitations mentioned restricted movements to broad, elliptical contours, except where knee and thigh contact intruded. [illegible] highest contour came to lie above the [illegible] shoulder. At the next section, there [illegible] not room for forearm and wrist movem[illegible] between the body and the reference pl[illegible] This limitation to hand movement [illegible] duced a definite posterior surface to [illegible] portion of the kinetosphere in front of [illegible] trunk region. Until the trunk hind[illegible] movement, knee and thigh contact and [illegible] maximum amount of abduction, flex[illegible] extension, or adduction permitted at [illegible] wrist joint were the limiting feature[illegible] movements in the coronal plane.

After trunk contact with the wrist [illegible] forearm, the only territory free for a[illegible] tional limb and hand movement was la[illegible] al to the trunk on the test-limb side of [illegible] body. These contours became narrow [illegible] tical ellipses, with the upper pole ten[illegible] to deviate toward the head. Movem[illegible] was restricted on the left because of [illegible] ability to increase wrist abduction. O[illegible] boundaries were due to limited wrist [illegible] ion (above), to the amount of wrist [illegible] tension permitted (below), and to [illegible] contact (medially). At the extreme p[illegible] rior range, shoulder retraction and el[illegible] flexion reached a maximum. It sh[illegible] be noted that the narrow seat back [illegible] did not restrict movement of the shou[illegible] and elbow and that the hand could r[illegible] about at the side of and even slig[illegible] behind the body without artificial con[illegible] restraints.

Total shape

Although serial sections are informa[illegible] the three-dimensional character of th[illegible] netospheres can be shown initially to b[illegible] advantage by reconstructed plastic m[illegible] els, such as that in figure 4. The m[illegible] represented a smoothed composite of [illegible] mean space envelope for the prone h[illegible] The principal bulk of the kinetospher[illegible] in front of the trunk and above the [illegible] and thighs, extending a full head hi[illegible] than the mean sitting height, and its m[illegible] imum height was again above the [illegible] shoulder. The kinetosphere bulged m[illegible] ally and laterally—mainly laterally—[illegible] it had a "wing" projecting to the left [illegible] backward to a point a little behind the [illegible] R-point. For the prone hand, much o[illegible] restraint medially and laterally was ca[illegible]

ig. 4 Medial view of a three-dimensional reconstruction of the mean kinetosphere for prone left d shown in relation to the seat and an average size subject.

the limitation of wrist adduction and luction. The larger range of wrist flex- and extension was less restrictive on hand at the upper and lower limits of hand range.

Vhen the grip axis is held vertically in- ad of prone, the limit due to wrist ab- tion affects the lower kinetosphere ge rather than the lateral side. When grip axis is supine, the abduction limit cts the medial side of the space. Simi- y, flexion, extension and adduction lim- of the wrist affect different parts of etospheres according to the angular ition of the grip axis and the orienta- n of the specific restraining ligaments. Each of the 8 kinetospheres studied was ilar to the extent that the major bulk the space was above the thighs and ad of the trunk and that each had a g to the side of the body; nevertheless, h had characteristic differences in dimensions, in height relative to the seat, in size of wing or in slope of contour in one region or another. These differences were basically controlled by the kinematics of the upper limb joints and segments under the restrictive conditions of holding the hand grip in a constant orientation.

Factors affecting kinetosphere shape

When confronted with a three-dimensional model of a kinetosphere, people sometimes suggest that the subject should be able to reach higher, more to the side or more between the thighs. This is true, but for the average test subject, it is true to a marked degree only when he fails to maintain the standard hand orientations. The conditions for defining a given kinetosphere no longer exist when a subject appreciably changes the grip orientation or the direction of hand "pointing."

The range of translatory movement permitted the hand by the upper limb joint systems was limited in different directions either (1) by contacts with the trunk, thighs, or knees, or (2) by a restriction of movement in one or more critical joints in consonance with the hand having a fixed orientation irrespective of where it lay within a kinetosphere. The joint limitations were just as real as the body contacts. When the hand moves about while it maintains a fixed orientation, the wrist, the forearm, the elbow, and the claviscapular mechanism of the shoulder, which lie between the hand and the trunk, must adjust to the movement within the limits of their individual joint ranges. In one part of the hand range, depending upon the orientation of the hand in translatory motion, further movement may be limited by the inability to abduct the wrist further while in another region a lack of additional wrist extension may be the restricting factor. Shoulder and elbow joints may limit movement in the same way. The boundaries of each kinetosphere thus are determined by a distinctive type of limitation.

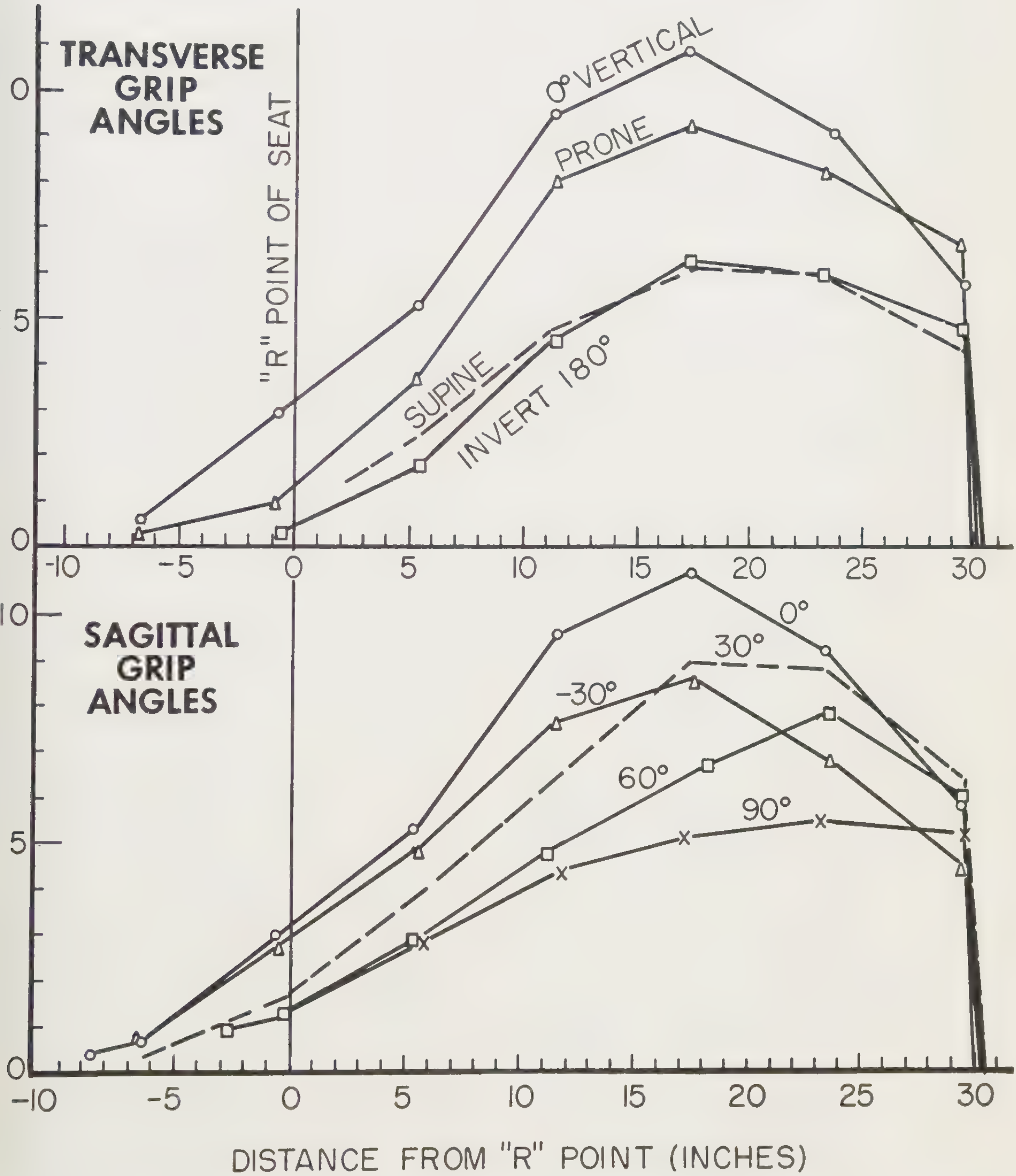
Linear dimensions of the upper limbs also are metrically correlated with the extent of hand range, thus the longer-limbed subjects were able to reach farther upward, downward, laterally, and medially across the trunk, as well as farther forward and backward. In general, tall, thin men with more flexible joints had greater hand ranges (Dempster, '55a), and smaller, heavier men with less joint flexibility produced kinetospheres of reduced dimensions.

Functional body contact must be understood as contact with any part of the arm, elbow, forearm, hand, or hand grip. Arm and forearm contact in one or another hand orientation affects the closeness of the grip point to the front and side of the trunk, to the groin region, to the medial sides of the thighs, to the opposite side of the thighs, etc. These contacts imply functional limits to hand range; since the grip point lies in the middle of the fist, it never can be closer to the body at any point than perhaps three inches.

Other factors having an effect on kinetospheres related to the psychology of the test individuals. If the subject did conscientiously attempt to reach the maximum of the translatory motion, kinetosphere boundaries proved false. the taking of records by the procedu outlined, it soon became apparent t overly eager subjects tended to bend trunk or twist the hand position to unreasonably large ranges. Neon lights a tached over the subject's sternum, ho ever, gave an indication of the degree this defect. Where the records showed a unusual amount of trunk movement, records were discarded and repetiti were made. Contrarily, lazy subjects te ed not to exert themselves. Careful att tion to procedures and repetitions, in tain instances, undoubtedly reduced t source of error to a minimum. The avera ing procedures employed smoothed most of these individual differences. Mea ures of variability, which will receive a tention below, clearly involved psyc functional factors as well as strictly ki matic factors.

The reference grid introduced an e trinsic, non-functional factor; it exten 5 in. on either side of the center of ball and 7 in. beyond. The contact of grid with the body was not a signific contaminant for the supine or the sagit series of kinetospheres. Figure 3, ho ever, suggests that if the reference g had not been between the hand and side of the body the medial border of "wing" might have extended inward m Overall kinetosphere volume, in this stance however, would be reduced only the region at the side of the body. invert kinetosphere was more seriou affected; if the grid were to be seen by subject unobscured by his hand and fo arm, the grid must lie between the thi and hand. The regions above, forward the sides, etc. were not affected by g error. The inclusion of partially conta nated prone and invert data in this pa may be justified since these extrinsic c tact errors are on the body side of kinetosphere rather than on the ou ranges; accordingly the errors have li effect on the problem of practical w space design. Questionable features, ho ever, will be kept before the reader.

The greatest discrepancies from sub-
t to subject related to the kinetosphere
ion nearest the thighs, pelvis and lower
nk. Frequently the subject did not move
hand as closely as possible over and be-
een the thighs; consequently, the clock-
se and counterclockwise circuits were less well duplicated in this region than in the rest of the circuit. The mean curves drawn in consequence appeared to be displaced upward by several inches. The subjects sometimes moved their feet from the foot rest and, by planting the feet flat on the floor area ahead of the seat, raised



g. 5 Two series of plots showing the panel area available to the grip point of the left hand for
sverse planes at different distances from the "R" point of the seat.

thigh height; in such instances the lower borders of kinetospheres would be raised still further. Practically, however, these discrepancies do not affect the exterior dimensions of the work space; they would affect only the region adjacent to the trunk and thighs. Kinetosphere volumes, centroid height and the height of common hand areas, etc., would be biased to a degree, but in a predictable direction. Except for the invert kinetosphere as mentioned, there is no reason to expect that the bias should not be the same for all hand orientations.

Area to distance plots

The curves in figure 5 are plots of the areas of cross-sections through kinetospheres relative to the distance of these cross-sections from the R-point of the seat. Each of the curves refers to a different hand orientation and is an average for the 22 subjects. The upper figure represents area/distance plots for transverse orientations of the hand grip and the lower shows plots for the sagittal hand grips. These two plots show, then, the relative maximum range of the hand (i.e., grip point) over vertical-transverse planes placed at intervals from 30 in. ahead of the R-point to 9 in. behind. If a worker such as a telephone operator were to be seated in front of a vertical panel, the area plots suggest the relative area of hand-panel contact at different seat-to-panel distances.

At the farthest extent of arm reach (± 30 in.), the cross-section within reach increased rapidly from zero to 400–700 sq. in. Areas at distances closer to the seat then built up to a maximum (600–1000 sq. in.) for the best distances from the R-point and then fell off rather rapidly. The curves for 0°, prone, −30°, and 60° rose rather sharply to a maximum; those for 90°, supine, invert, and +30° built up more gradually. Since the size of the hand grip introduced a bias (discussed above), the prone range should be slightly higher at the side of the body (i.e., +12 in. to −7 in. in relation to the R-point). The more anterior range for invert should read higher. All of the curves fell off rapidly inside the +12 in. level. The 90° curve showed fairly constant panel areas of ±500 sq. in. between 15 and 30 inches from the point; closer to the R-point, the ar dropped off rapidly.

In general, the areas indicated by the curve were larger than the others; 0° lowed by prone, +30°, −30°, and 60° maximal areas in the 800–1000 sq. range. The curves for invert, supine, 90° were definitely less.

The maximum area covered at a gi distance from the seat varied accordin hand orientation. Most of the cur showed maximal cross sectional areas 17–20 in. from the R-point; for the to 90° hand orientation, the maxima w closer to 24 in. from the R-point. Th section-to-R-point distances referred to horizontal distance from the R-point to grip point; when in a practical work-pl situation, objects in the fingers and ha protrude anterior to the grip point; due lowance should be planned for this ad tional dimension.

Kinetosphere volumes

By measuring the areas under the ar distance plots with a planimeter, it possible to obtain the volume of any gi kinetosphere. Thus, we had a further terion for demonstrating the characte tics of different hand grip angles. Th volumes are presented in table 1, wh

TABLE 1

Average kinetosphere volumes for the study gr

Hand orientation	Volumes	Hand orientation	Volu
	cu. in.		*cu. i*
−30°	19,990	90°	13,040
0°	24,630	Supine	13,180
30°	19,940	Prone	20,670(
60°	13,030	Invert	12,920(

shows the kinetosphere volume for 8 ha positions.

Attempts were made to correlate lin dimensions of the subjects and gonion ric data on the ranges of joint flexibi for the upper limb with the volumes kinetospheres of individuals; these show a general correlation between volume the work area and both body size and amplitude of joint movement. Neit standard anthropometric measureme nor measurements of joint range alc however, presented the whole story si individuals differed notably. Large n

h low joint flexibility or small men with ater joint ranges showed no consistent ume patterns.

Kinetosphere sections

The illustrations of figures 6 and 7 re- sent averaged sections of the 8 hand etospheres for the test subjects. In h instance, the kinetosphere is correct- placed relative to the "R" point of the t; thus shapes, centroid positions, etc., 1 be compared relative to the seat. For h kinetosphere, the three sections cut ough the mean centroid location for 22 men; the small crosses show the ation of the mean centroids relative to seat. The sections are perpendicular one another; for each set of three sec- ns the figures show, from left to right, ransverse, a coronal, and a sagittal sec- n through the centroid. Patterns for h right and left hands are shown in the (transverse) and front (coronal) w; these represent in reality a direct d mirror image of the left side kineto- eres.

The earlier section on technique indi- ed how the centroid of a kinetosphere s obtained. The centroid or center of vity for a given kinetosphere has a spe- c location above, ahead of, and to the e of the "R" point of the seat. It is mean center of all the possible grip nt positions for the given grip orienta- n—the point from which the hand may the average, move farthest in all direc- ns. Except for the 60° and 90° kineto- eres (figs. 6 and 7) where it is low, centroids for the different kineto- eres lie above shoulder height, lateral the shoulder and behind the knee. e locus of the invert centroid, which s influenced by hand-appliance contacts, pictured too high by perhaps 2 in.; if lower contour of the original frontal tions were to be lifted by 5 in., the troid would be elevated 2 in.) Each ation is distinctive according to kineto- eres, but there appears to be an under- g similarity. Figure 8 implies that each troid is an expression of the hand po- on that results when each upper limb nt is fixed at the mid-range of its joint plitude. The specimen illustrated was special joint-ligament dissection; each joint between the clavicle and wrist was anchored at the mid-range position for each type or degree of freedom of joint motion permitted (joint range data from living subjects, Dempster, '55a).

In spite of the general similarity in contour of the top views, a number of differences can be seen. From 0° to 90° (sagittal grip orientations), there was a marked decrease (fig. 6) in both the size of the kinetosphere and in the overlap of right and left hands. In addition the midline region of the kinetosphere moved farther and farther from the body. Although the centroid of each of the 8 kinetospheres was in approximately the same position, anterolateral to the seat, there was again some variation. From 0° to 90°, the centroid moved progressively farther out to the side. The 0° centroid was slightly closer to the "R" point of the seat, but the others were at about the same anteroposterior distance. Lateral reach was approximately the same for all the sagittal hand positions. The same held true for the distance back that the subject could reach. The kinetosphere for −30° was generally intermediate to 0° and +30° in size, in overlap of right and left hands, in centroid position, and in proximity of the kinetosphere to the body at the midline.

In the transverse hand positions (fig. 7), kinetosphere dimensions were less for supine and invert than for 0°, in fact the smaller kinetospheres were about the same as the 90° kinetosphere; that for the prone hand approximated the size of the −30° and +30°. The amount of right-left overlap increased and the distance between the kinetosphere and the body in the midline region decreased to 0°; the supine kinetosphere contrasted markedly in both respects. The lateral position of the centroid remained about the same from invert to 0°, but it was far more lateral at supination (approximating that of the 60° kinetosphere). The distance of the centroid from the "R" point decreased through invert and prone to 0°, though it increased again at supination. Hand reach laterally and posteriorly toward the "wings" of the kinetosphere was reduced for the invert, prone, and supine hand positions, although lateral reach was slightly greater for the invert kinetosphere. (The reduced medial

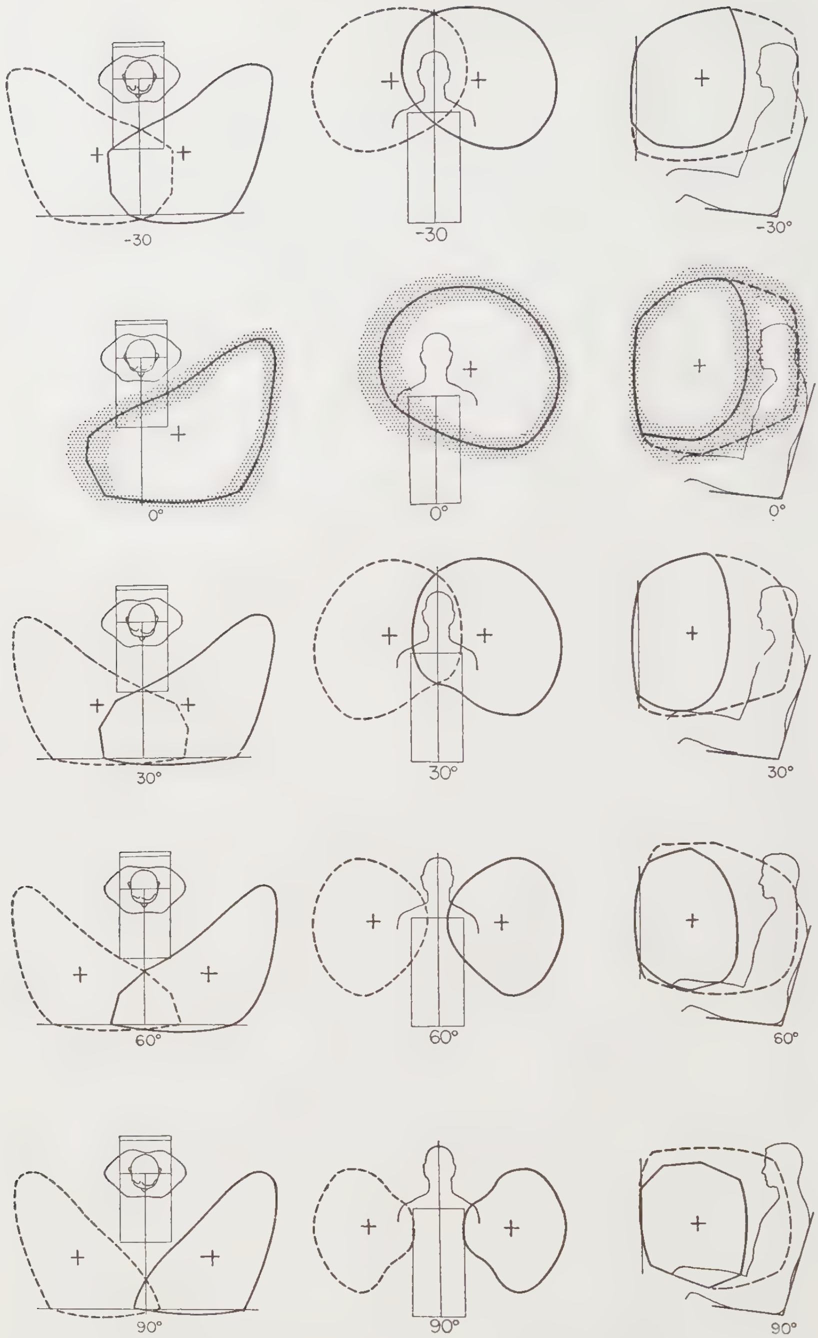
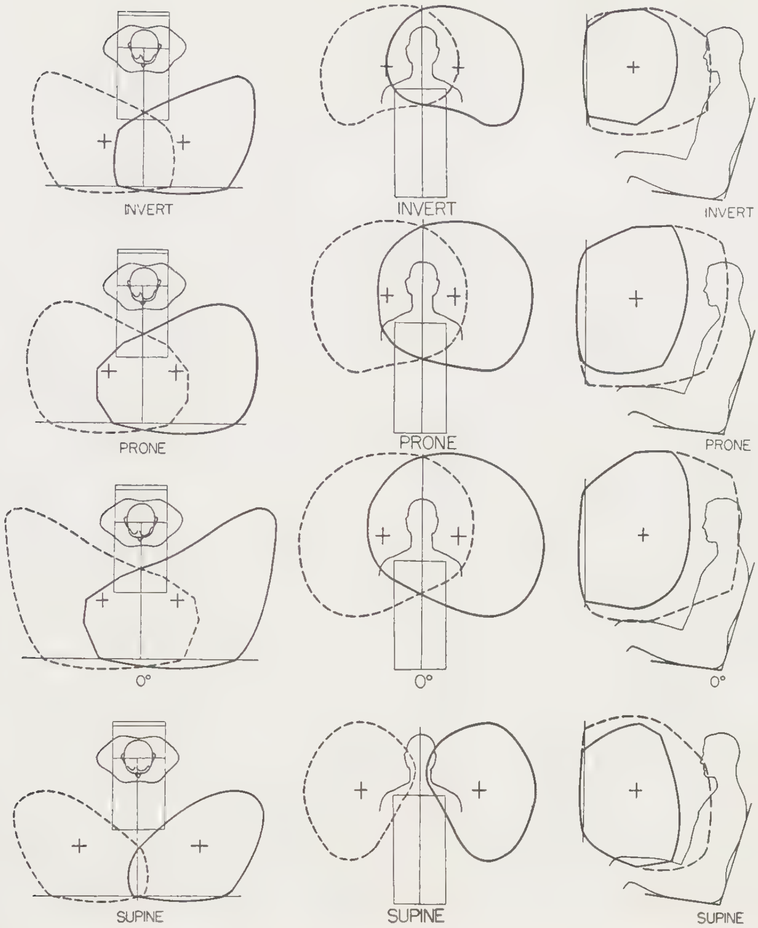
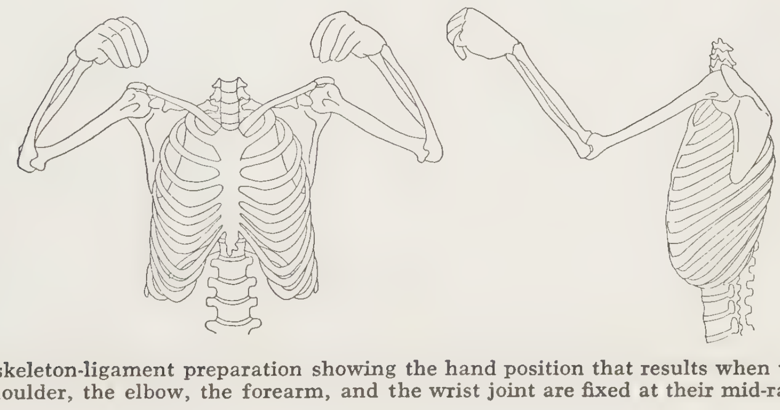


Fig. 6 Top, front and left side view of sections that pass through a series of kinetospheres at centroid level. Each successive transverse row represents 30° additional tilt to the hand grip in the sagittal plane. The right side areas are mirror images of the left side. The shaded halo for the 0° kinetosphere illustrates the mean deviation for different regions of the contour. A plus sign shows the location of the kinetosphere centroid.



.g. 7 Top, front and side views of sections through kinetospheres representing transverse changes he grip axis.



g. 8 A skeleton-ligament preparation showing the hand position that results when the sternoclav-ar, the shoulder, the elbow, the forearm, and the wrist joint are fixed at their mid-range positions.

border of the wing for the prone kinetosphere was in part artificial because of hand grid interference.) Contrary to the sagittal grip positions, the transverse grips, other than 0°, did not allow the average subject to reach back posterior to the "R" point.

The front views of the kinetospheres demonstrated about the same sequences and variations as the top views in regard to size, reach, and overlap. There was, however, no overlap at the centroid level for supination, 60°, or 90°; the overlap region was farther forward. From −30° to 90° (grip orientations in the sagittal plane), there was a marked decrease in centroid height, which was below the shoulder at 60° and 90°; no clear sequence was found in the transverse plane. The centroid heights for invert, 0°, and prone were above the shoulder in that ascending order—invert was artificially high because of hand grid interference; that for supination was right at shoulder level.

In the side views of the kinetospheres, the solid line represented a section through the centroid; the dashed line indicated the maximum contour to the side of the centroidal section—through the "wing." The main feature to be noted here is the vertical dimension of the lateral extension or "wing" of the hand kinetosphere. In the side views showing −30°, 0°, and +30°, the lateral projection extended below the main body of the kinetosphere, but not above; at 60° and 90°, it extended both above and below. For the transverse grip orientations, the lateral extension was again lower for invert and supination than for 0°. The respective heights of the kinetospheres themselves again were revealed in the side view; the lower border of the invert kinetosphere would appear to be too high. It may also be noted again that transverse hand orientations do not permit much posterior projection of the kinetosphere.

Surrounding the outlines of the 0° k netosphere in figure 6 are halos which rep resent the mean deviation of the 22 sub jects of the test sample. The 0° kineto sphere was the least variable of the kineto spheres from region to region and from subject to subject. In addition to mean de viation, standard deviations were compute for superimposed horizontal and sagitta section contours of the 8 kinetospheres fo the 22 subjects. The variability relative t the mean contours was measured in places along radiating lines from mea centroid to the contours. Measurement were made along an antero-posterior lin through the mean centroid and along line through the centroid at equivalent 60°, an 120° angles to the right and left; thes lines cut the contours at 6 points alon their circumference. The standard devia tion of these measurements, as compute gave some measure of the relative variabi ity of the kinetosphere contours relative t one another. The values of the standar deviation and of the range which include 90% of the hand positions (in parenthe ses; i.e., 5th–95th percentiles) are show in table 2. This tabulation shows that th 0° kinetosphere was least variable, that th −30° and the +30° kinetospheres wer slightly more but similar in variability, an that the 60° and 90° kinetospheres were in creasingly variable—the 0° was about 60% as variable as the 90° kinetosphere. Th prone kinetosphere had a slightly large standard deviation than the −30° an +30° kinetospheres, the invert hand or entation had more, and the supine was th same as the +60° kinetosphere. Thes values in themselves are of little impor ance, but there are significant implicatio relative to the placement of hand contro for the seated operator. Because of th variability between subjects, more critic placement of controls in the work place necessary when planned for the 90°, 6 and supine positions of the hand than

TABLE 2

S.D.	90% Range	S.D.		90% Range
−30° ± 3.2 in.	(± 5.3 in.)	90°	± 4.7 in.	(± 7.7 in.)
0° ± 2.8 in.	(± 4.6 in.)	Supine	± 4.2 in.	(± 6.95 in.)
+30° ± 3.3 in.	(± 5.45 in.)	Prone	± 3.5 in.	(± 5.7 in.)
+60° ± 4.2 in.	(± 6.95 in.)	Invert	± 3.8 in.	(± 6.75 in.)

e 0°, +30°, −30°, and prone hand orientations.

Strophospheres

When sections through a related series kinetospheres were superimposed toproce a strophosphere, a larger space was tlined than that for any individual kitosphere (figs. 9 and 10). The kinetoheres were superimposed relative to the it and "R" point. Figure 9 shows a ophosphere which defines hand position th three degrees of translatory freedom motion plus one degree of rotation in e sagittal plane through angulations of 30° to +90°. Figure 10 shows another ophosphere in which the hand grip ro-es through the transverse plane (from pine through 0° and prone to 180° inrt), in addition to the usual freedom for nslatory motion. In both figures, the nds that were noted earlier when sepate kinetospheres were compared can seen.

The size of the hand space for the 0° entation decreased systematically in sevl respects through the sequence 0, −30, 30, +60 to +90°. The postero-medial e of the strophosphere, i.e., toward the bject, shifted forward with each new nd orientation to reduce kinetosphere e. The wing decreased slightly, and the gion of right-left overlap decreased markly. Furthermore, the rear of the overlap ea came to lie farther and farther from e body. The relative height of the upper d lower contours, including those of the ng, came to lie lower and lower through e series: 0, −30°, +30, +60, and 90°. Both the frontal and sagittal secns showed this sequence.

Similar transitions were shown for the nsverse series of kinetospheres. The pine kinetosphere occupied a small part the strophosphere. Its height was low, e shape was globular, and the wing was duced in size. With the vertical (0°) nd orientation, the wing, the medial read, and the right-left overlap increased a maximum; the height of reach ineased notably. For the prone hand, both e wing and the amount of right-left hand erlap were somewhat reduced. These nds continued further for the invert nd orientation (180°).

The strophosphere plots emphasized differences due to hand orientation, but, more importantly, they pointed to common features in a new way. The horizontally shaded area of figure 9 shows the space common to all vertical hand orientations; similarly, figure 10 shows the common space for all transverse orientations. For the sagittal hand orientations, the side-to-side, and especially the up-down extent of the common region was reduced; the posterior extent of the strophosphere wing, including the common region extended back to the "R" point. For the transverse hand orientations, the common hand space is short of the "R" point by about 12 in.; it corresponded most nearly with the region within reach of the supine hand, but its lower range was less extreme.

The dots shown in figures 9 and 10 show the location of the centroids of the kinetospheres that were grouped in each of the strophospheres. In general they form graded sequences from kinetosphere to kinetosphere; they fall mostly above the distal part of the thigh, to the side of the shoulder and above the shoulder. The invert centroid (fig. 10; 180°) may, for technical reasons, be shown too high.

The region common to both the sagittal and transverse orientations of the hand, as seen in frontal and sagittal sections (fig. 11), was only slightly reduced from the size seen in the separate strophospheres. In horizontal section, the common area for the 8 hand orientations studied was reduced near the body and in the wing; the posterior extent of the common area of the wing was about 6 inches ahead of the "R" point.

The common region (fig. 11—heavy stippling) was roughly 15 inches wide, 16–18 inches high, and 18–24 inches deep; it lay obliquely, and its maximum anteromedial to posterolateral extent was about 30 inches with a perpendicular breadth of 18 inches at the maximum dimension. The orientation to the seat, to the "R" point and to a man with the dimensions of our average subject, is shown; the body size shown is a composite based on tracings of photographs of the 7 subjects in our sample who most nearly corresponded to the average in sitting-height, sitting-acromial-height and stature. The right-left

overlap was negligible and far forward; most of the space was lateral to the shoulder region. It extended from nose to waist level and from the line of the chest forward to the extent of maximum hand reach. Within such a range, the forward-directed hand could supinate or pronate through some 270° and could rotate in the sagittal plane to about 120°; presumably, movements about a horizontal transverse wrist axis for various degrees of pronation and supination also should have been possible throughout most of the region.

Our figures have defined the region *par excellence* for the positioning of hand controls to be operated by one hand. Within this range there may very well be regions of preference, or regions of greater or l[illegible] ser strength, or regions better correla[illegible] with precise or with gross movements, [illegible] regions more central relative to the vis[illegible] field. Further study in this respect sho[illegible] have value practically. (For instance[illegible] separate study on the mechanics of str[illegible] two-handed pulls for the seated opera[illegible] (Dempster, '58) has shown that irresp[illegible] tive of the position of the hands, the p[illegible] vector is always (except for weak pulls[illegible] directed toward the midsternal region; t[illegible] implication is that when levers and h[illegible] dles are placed in the work area, the dir[illegible] tion of pull be planned as intersecting t[illegible] sternum.) Regions outside the comm[illegible] range will not permit completely free mo[illegible] ments of the hand. Closer study of the r[illegible]

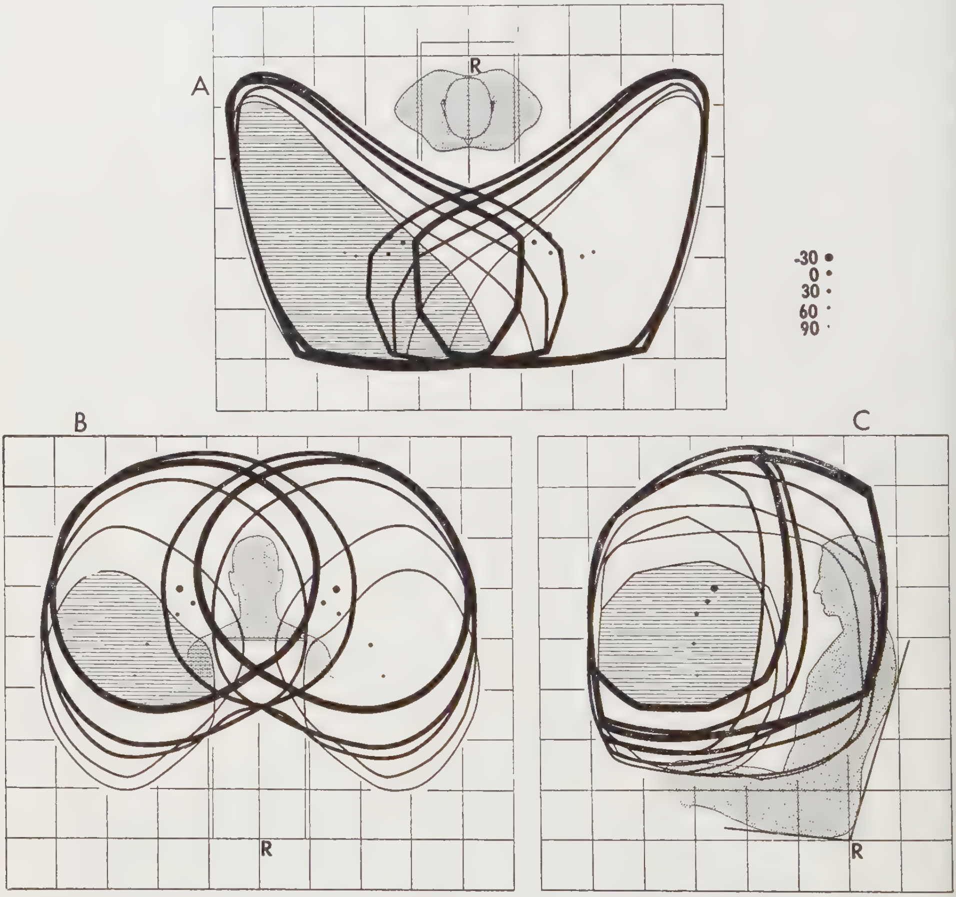
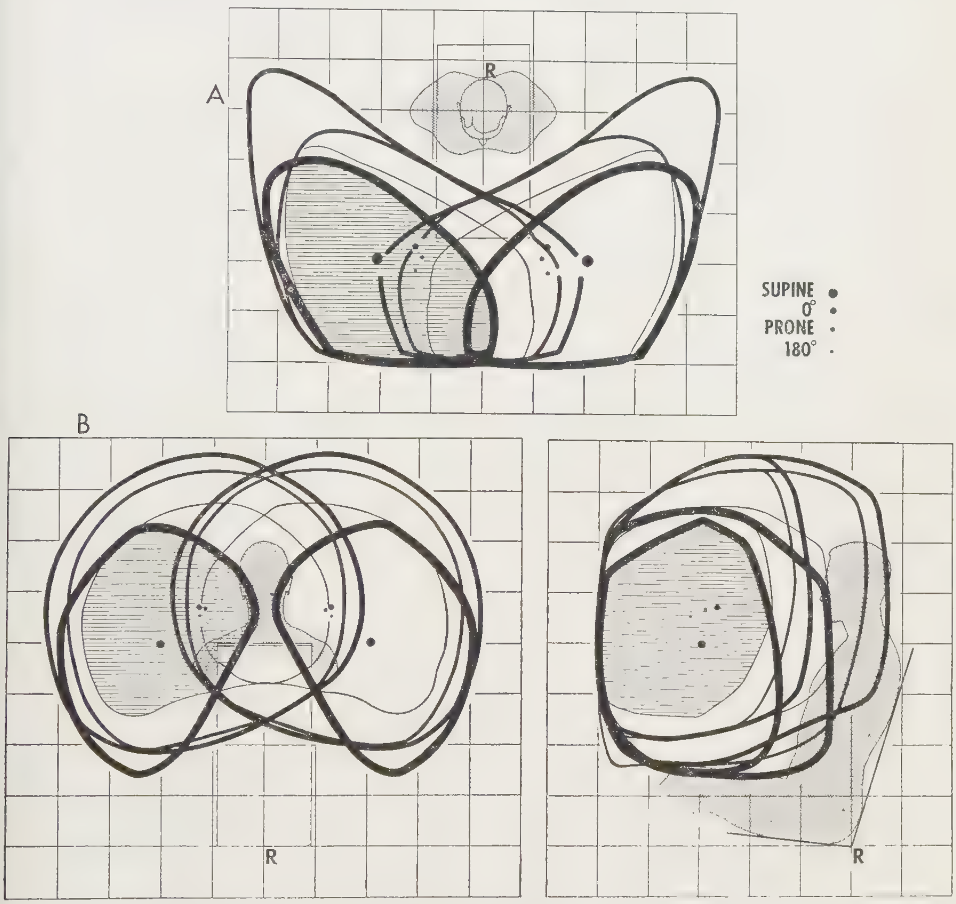


Fig. 9 A group of superimposed kinetospheres representing changing grip orientations in the sa[illegible] ittal plane enclose a strophosphere. Horizontal shading, the region common to each kinetosphe[illegible] dots, centroids of the several kinetospheres.

es showing the common region of the ophosphere in relation to specific work erations might suggest certain restric-e hand positions not be used; the com-on space for other hand positions would larger than if the restrictive positions re included.

A centroid for a given hand orientation plies the most central position within a netosphere. It is the least restrained sition, or mean average position, for the en hand orientation relative to the ole system of limb joints. As in the ady or defensive position of the fists in xing, the centroids (dots, figs. 9, 10 and) represent a sort of mean starting posi-n for hand movements toward the limits the reach in any direction. The cluster of centroids representing the different hand orientations studied should have similar implications for the combined strophospheres or ergospheres.

The centroids are shown in figures 9, 10 and 11 as clusters of points relative to the contour of an average-sized man. The centroids as seen from the side view were more or less vertical within a range of 15–19 in. from the "R" point; from above, the centroids extended from side to side in a band 7–15 in. from the midline; the front view shows the points extending in an oblique direction from above and medially (30 in. above the "R" point of the seat and 7 in. from the midline) to a lower and more lateral point (15 in. from the midline and 19 in. above the seat "R"



ig. 10 The strophosphere resulting from superimposition of a transverse series of kinetospheres. izontal shading, the common region for hand motion; dots, the location of kinetosphere centroids.

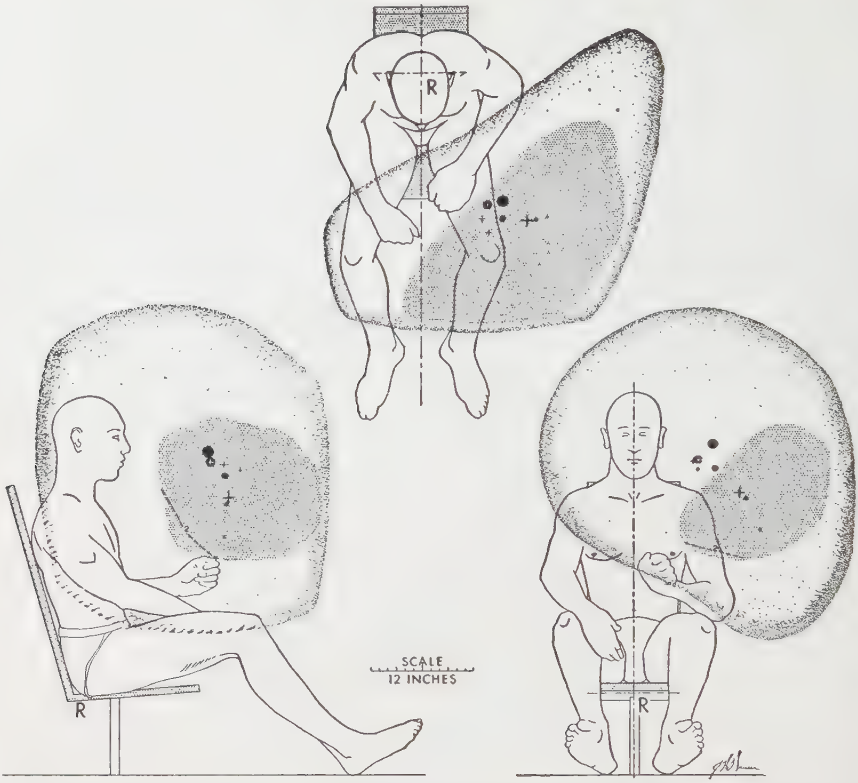


Fig. 11 Combined transverse and vertical strophospheres showing the common region for 8 ha
orientations.

point). Relative to the average size subject, the cluster extended from nose tip or ear height to the lower end of the sternum; the centroids lay above the distal third of the thigh 2 1/2-6 in. posterior to the knee. The cluster of points extended obliquely from above the shoulder at the lower face level along a 45-degree angle downward and outward.

The segments of the limb have weight, and some muscular effort is required to support the limb in its various postures. This implies fatigue when the effort is prolonged. Muscular effort, however, is virtually eliminated when the hand hangs freely at the side of the body or when it is supported on the thighs or upon some surface such as chair arms or a work table or desk. The hand positions associated with these postures may be of primary practical importance as starting positions for hand motions.

DISCUSSION

Although figures 9 and 10 have be scaled off on a 6-in. grid (and fig. 11 wa drawn to the same scale) it would be mistake to assume that the dimensio given would provide more than a guide f the designing of a practical work spa The information derived from our stu involves a specific sample of subjects a a set of experimental conditions whi have been described above. Our aim this paper has been twofold: (1) to dev op an indirect approach to a functional a thropometry in the hope that further stu ies will produce still better answers, a (2) to present data which, if intelligen handled, should contribute to the desig ing of more effective work places, cockp and driver compartments.

It would be entirely unnecessary to ev think of gross work space dimensions a cell or compartment the height of

rker and with a floor area 6 ft. (side to le) × 3.5 ft. (front to back), i.e., slight- larger than the grid of figure 12, could provided. When, however, as in a hicle, the available space must be re- ced or when an efficient layout is im- rtant, an evaluation of the different gions within reach is warranted. Plans a work space based upon our stropho- heres may form part of a solution but to rve practical ends, it will be necesary to scuss several additional points:

1. The only kinetospheres (and stro- ospheres) that we have studied involve forward aiming of the hand—the hand d was initially set with the arm hori- ntal and pointing forward from the oulder; all 8 hand grip orientations on ich data were obtained were dependent this one condition. If, instead, the left nd had been directed toward the right e., bent elbow) a strophosphere space a tle more than shoulder width and from e lap to the top of the head would be cluded (heavy dashed line bounding ace "A" in the three sketches of fig. 12); e fore-to-back extent would be about e same as the width. The region of right- t overlap would include almost all of is new strophosphere space. Obliquely- rward hand orientations would inter- ade from this region to that described ove in our study. If the strophosphere re to involve a downward pointing of the nd, the grip-point space would extend om shoulder height or lower to just below at level. If the hand were to be directed terally, the associated kinetospheres uld lie entirely to the side of the trunk d there would be no right-left overlap; e hand space would lie almost wholly thin our strophosphere spaces; it would, wever, bulge several inches more lateral- (arm span, fig. 12, M). The upward-di- cted hand would likewise be largely with- our kinetospheres (from chest height ward), but it would reach several inches gher. Precise predictions of space in- lved for the different hand postures can- t be made without accurate data and a tailed analysis. None of these additional rophospheres, however, would extend as r forward as those of our study.

2. An actual practical work area must addition to room for hand movement provide space for the operator's body. The basic unit of the work area is the seat, and its "R" point provides a suitable origin for the coordinate system to which dimensions are scaled. Since body stability is an es- sential for hand actions, seating area, seat height, floor area (Dempster, '55a), foot supports and the locations of foot controls all require careful planning. Despite sev- eral studies on seating (Lay and Fisher, '40; Randall et al., '46; Åkerblom, '48), no adequate statement of the mechanical principles involved in seat stability has as yet appeared. Seat backs, head rests, har- nesses, arm rests, etc. are also involved with body stability. The planning for a specified man-machine operation should call for a total functional-mechanical an- alysis of work motions. Provisions for body stability, however, cannot be made secondary to those concerned with the placement of controls, equipment and par- aphernalia. The work place must always have a convenient path for entrance and exit (shaded arrows "B," fig. 12).

3. The original data were derived from subjects for whom the heel-to-eye height was fixed at 39.5 in, as in the "fighter" cockpit. Thus the seat-to-floor distance was less for tall men than for shorter ones. The average seat height was nearly half that of a kitchen chair. The major dif- ference between the high and the low seat, as far as the work place is concerned, is the relative spatial position of the feet relative to the manual space. If the floor area is adequate for the bracing action of the feet, body stability should be about as good in a chair of ordinary height as in the cockpit; then hand reach should be comparable in the two situations, and no discrepancies should be anticipated in the planning of a work area for seats of ordi- nary height. If the tilt of the seat back were notably more or less than the 17° from vertical of our test seat, the fore-to- back location of the shoulders relative to the "R" point (and the several kineto- spheres too) would be displaced slightly.

4. When our subjects sat upright in a balanced position with the trunk away from the seat back, the shoulders shifted forward an average of 2.5 in. relative to the "R" point. Thus for a worker on a stool (without a back), each kinetosphere

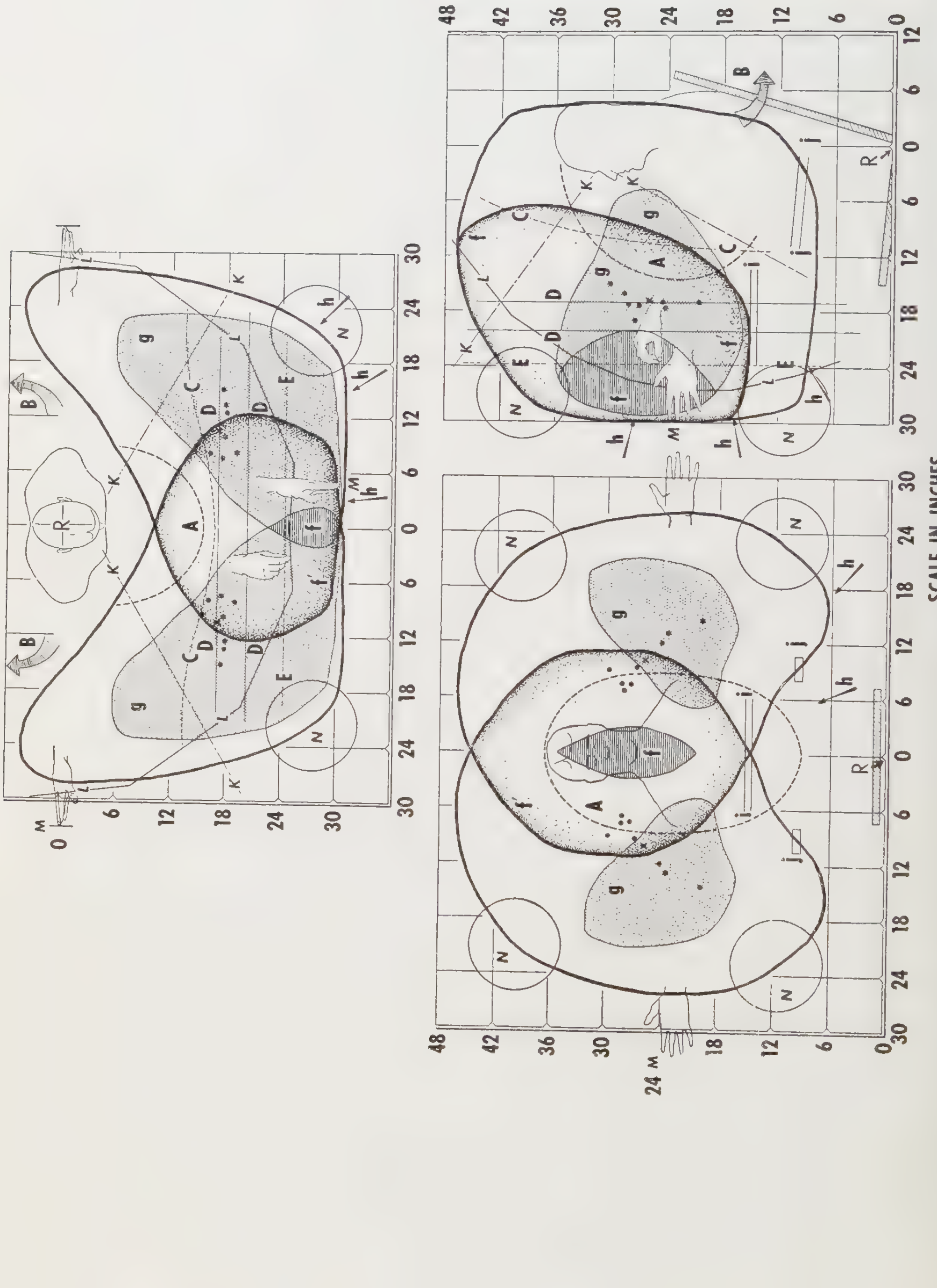


Fig. 12 A work space plan based upon the kinetosphere-strophosphere analysis of the forward directed hand.

d the whole hand space is moved for-
ırd a predictable amount.

5. If an operator sits on a settee, as in ɜ automobile, the backward movement his elbows is limited by the seat back, d the potential hand space (roughly the gion behind the dashed outline "C," fig.) is unavailable.

6. Planning of the work area implies th a fixed chair position and a fixed ıcement of knobs, levers, cranks, im- ɜments, bins, etc. The chair distance d height may be adjustable to a degree r individuals of large or small size but ese changes should be planned in ad- nce. In "fighter" aircraft, for instance, oblique up-and-back/down-and-forward justment has been employed to keep e height constant and to provide a suit- le pedal-to-seat distance.

7. If an operator were to sit before a ınsverse panel, he would be able to reach ɜ largest possible area if the panel were t 17 to 20 in. ahead of the "R" point (fig. , D-D). (The panel distance refers to " point to grip point, and, in practical plication, an additional distance "X" ll relate to fingers or objects in the nd, etc.) For the 90° grip position (i.e., tero-posterior grip axis), the mean panel stance would be 24 in. (fig. 12, E).

8. Our kinetospheres were defined as ɜ outermost surface that the "grip point" ɔuld reach for the conditions tested. sh buttons or finger switches could be ıced about 3 in. farther anterior, and ɜy would still be within reach since the ger tip positions are about this distance advance of the "grip point." The re-de- ed anterior surface of the work area ɔuld be understood as an outside range r placement of switches, knobs, etc. with- convenient reach of the operator (with- t the necessity of his moving his trunk).

9. One may assume that critical or ɜquently used or emergency controls ɔuld be more accessible in the work ɜa than items of occasional use. The gion of right-left overlap of our kineto- heres (fig. 12, f, horizontal shading and marginal stipple) and the more proxi- al region "A" in the figure would have rtain advantages.

Similarly, the region common to differ- t hand orientations (fig. 12, g, stipple) which is contiguous with "f" should be of maximum utility. The more proximal region "A" in which different orientations are possible also should be important. In addition, the region near (and slightly below) the kinetosphere centroids (heavy dots, fig. 12) defines a position of high flexibility. The "X" within the cluster of dots represents the mean strophosphere centroid and the locus of this point in three dimensions relative to the R-point should be noted. (The three projections of figure 12 are based on strophosphere sections which intersect at point "X.")

10. It is equally important that free movement of the limbs not be impeded by the faulty positioning of parts. McFarland's study of driver compartments in commercial automobiles (McFarland et al., '53) emphasized that levers and controls have too commonly been placed so that they will neither accommodate the dimensions of men above average size nor permit free hand and foot movements. An illustration by Dempster ('55a, fig. 88) shows how foot movement is restricted when the knee cannot be raised beyond specified limits.

11. When the operator pulls a lever or hand grip toward his body, the most effective direction is toward his sternum (arrows, "h," fig. 12; Dempster, '58).

12. The table height and arm-rest positions ("i" and "j") shown in figure 12, represent conventional heights above the "R" point; measurements of elbow rest height by Hertzberg et al. ('54) are pertinent. Suitable arm rests (including table, steering wheel, etc.), if they do not impede necessary motions, should have value in reducing fatigue.

13. Several types of visual field (monocular field with fixed foveal focus, binocular field involving eye movement by ocular muscles, etc.) have long been recognized (Hering, '42). When the head is fixed but orbital muscles are free to move the eye, the visual field of each eye is framed above, below and on the nasal side by the eyebrow, cheek and nose. These parts of the facial anatomy combine to frame on all sides the composite field for precise binocular vision; in effect, this frame provides a hollow cone through which the subject looks. When the head is held in a fixed

position, the sides of the cone diverge from the principle line of sight by about 60° in all directions; a cone of 45° radial divergence would probably include about 90% of people (Schneller, 1875; Hering, '42; Giroud, '57). If the head is oriented so that a horizontal plane cuts the right and left tragion and the left orbitale, it is said to be oriented relative to the Frankfort plane; when the head is so oriented, a horizontal plane cuts the cone so that 45° of the purview lies above and 75° below (Giroud, '57; a 30°/60° ratio would include most people). Figure 12 ("k") shows that when a subject with an average sized binocular field for precise vision looks straight ahead with the head horizontal (i.e., on Frankfort plane), he does not see the whole work space without turning his head. He sees the region of right-left overlap, the common region for different orientations of the hands and the centroid positions of the hands. The whole work space including the wings may be seen by turning the head (Danielson, '58). It should be apparent that if the essentials of a work operation are positioned within the K-K cone that only minimal head movements need be used. If the operation must be performed on a table the head and K-K cone will be tilted downward; focal distance, convergence, near-to-far-distance visual shifts and other factors may also call for attention.

14. Our strophospheres were derived from young men whose dimensions averaged a little higher than the mean of the average population. If a work area were to be planned for women of average stature (5 ft. 4 in.), the various dimensions from the "R" point must be reduced by an appropriate ratio. A comparison of certain dimensions of male flying personnel and basic trainees with college and Air Force women (Wilder and Pfeiffer, '24; Daniels, Meyers and Churchill, '53; Daniels, Meyers and Worrall, '53; Hertzberg et al., '54) suggests that a reduction of our measurements by 6% would be a working approximation for the average female if joint flexibility is of the same order. Intermediate percentages or extrapolations beyond our measurements should be appropriate for special male worker groups.

15. The only previous measureme
on work area dimensions are those of K
et al. ('47). The dotted line "L" in fig
12 shows the extent to which 97%
King's subjects could reach their fin
tips. Forward arm-reach data (with sho
der protruded) for 97% of a test popu
tion (Hertzberg et al., '54) are shown a
at "m" (outstretched white hand) in
figures. (The functional pinch-reach w
shoulders back—also shown as a wh
hand—was shorter by 6 inches.)

16. When similar kinetospheres fr
different subjects are compared dim
sionally, the boundary limits of the kin
ospheres show intersubject variability d
to differences in build, in kinematic
havior and in psychology. The circles
5 in. radius (fig. 12, "n") suggest the or
of magnitude of differences in the po
tions of boundary limits that would rel
to about 90% of the subjects.

Several authors (McFarland et al., '5
'58; Hertzberg, '56) have argued that wh
members of a population are to be fitte
the dimensions of the 10th to 90th or 5
to 95th percentiles should be used inste
of the average. The use of the 90th
95th percentile dimension will be obvio
when the minimal clearance space f
larger people is involved; the difference
range between a high and a low percent
value should be important too in predet
mining dimensions for adjustments su
as seat position or seat height; but it i
questionable whether this principle ne
apply rigidly to a work area concern
with hand motions. Here we are deali
with flexible rather than with fixed ch
acteristics. The work area problem is o
that relates to the efficient placement
controls and equipment rather than to t
mere enclosure of a person who is a me
ber of a population; the extreme limits
the usable space are of little importan
for frequent motions, they are of mo
concern for storage and for the placeme
of rarely used controls. The subject shoul
however, be able to reach conveniently t
boundary limits of the ergosphere. If u
restrained by tight shoulder harness, slig
body movements should permit any norm
adult to reach the limits of our work ar
—forward and to the side (but not, f

ıe smallest people, upward). By bending is trunk, an operator should be able to each about 15 in. forward and 9 in. to ıe side without becoming unbalanced. A etailed job analysis should determine hether average or enlarged work space imensions are needed.

17. The initial one fifth-scale tracings f our photo records involved a clockwise nd a counterclockwise hand circuit of a low-lamp over the grip point. The two ırves at places often coincided while at hers either the clockwise or counter-ockwise was outermost. The mean dis-nce between the two circuits measured 8 points on their circumference (at 45° tervals) for a plane above the knees and nother over the thighs, 12 inches more osterior, was 1.4 in. The difference be-ween the mean curve we drew in to pro-de data for our original kinetospheres d the actual light traces was thus ±0.7 . The subjects often overshot the kineto-here boundary by this amount. Twice e S.D. was ±2.14 in.; thus about two-ths of the ±5 in. variability factor men-oned above (paragraph 16; fig. 12, "N") ould easily be within the reach of any bject without extraneous trunk move-ents.

Dimensional differences in limb seg-ents, differences in joint range and dif-rences in control due to handedness ould be expected between the right and t sides of a subject. When we arbitrarily udied motions of only the left hand, our easures of variability could not be ex-ustive.

18. In two instances, prone and 0° ki-tosphere records for the forward pro-cting hand were taken on standing sub-cts. The general shape and location of e kinetosphere relative to the trunk were ughly comparable to those for the same bjects seated; the principal difference is that the knees and thighs did not erfere and that the kinetospheres had a ooth convex contour below reaching to e level of the pubic symphysis. The rward and left lateral ranges were re-ced slightly since the trunk swayed in e opposite direction when the upper limb ıs stretched out in the more or less hori-ntal positions.

McFarland et al. ('58) remind us that a workman does not live in a vacuum nor in an ivory tower; he operates in an environment of ponderable things. We should not ignore even the weight and inertia of his own body parts. Man-machine systems are complex and the requisite background for effectively designing work areas and the placement of controls will involve: (1) more and better data on body kinematics and dynamic anthropometry (like those we have explored in this paper), (2) further information on body size and clearance tolerances (including measurements on women), (3) improved measurements on strength in relation to posture and stability and, (4) increased knowledge about the energy expenditure (i.e., rate of oxygen utilization) involved in different tasks. Furthermore, the actual confirmation of drawing-board plans must involve real people as subjects. Such intangibles as comfort and fatigue and such specific job features as the purpose and character of the work, production schedules, motivation, noise and safety hazards will continue to provide appreciable areas for compromise and practical judgments.

SUMMARY

The anthropometry of the manual work area was approached by an indirect method using photo records of time exposures showing the motions of a tiny neon lamp at the hand grip. The records of 22 male subjects were analyzed for 8 sets of motions involving the forward-directed hand and different grip orientations. Techniques were developed for defining the limits of the space within reach relative to the mid-sagittal junction of the seat and chair back. Graphical records of the different hand-range spaces were grouped and compared to bring out variability data, the extent of right-left hand overlap, regions of maximum hand flexibility, mean hand positions, etc. The data have been discussed in relation to the geometry of the more effective hand positions and in relation to practical problems of work space designing.

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ommunalities of the Ossification Centers of
ıe Hand and Wrist

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The bony nuclei of the hand and wrist, seen in radiographs, have long been conıdered as indicators of maturational status 'ryor, '06, '16, '25). Variously, attention ıs been directed to the time of appearance individual centers (Flecker, '42; Pyle ıd Sontag, '43; MacKay, '52; Wilkins, '50; ashburn, '51; Stuart and Stevenson, ł), to the number of centers present ontag, Snell and Anderson, '39; cf. heson, '54), and to combinations inlving number, size and extent of modelıg of ossification centers of the hand and ist (Flory, '36; Todd, '37; Acheson, '54; eulich and Pyle, '50, '59).

A perennial problem has been the emasis or weighting entitled to particular nters of ossification. One bony nucleus ıy be a far better indication of ossifican status than another, a particular epiysis or round bone may meter the develment of the hand and wrist, while yet hird may have little in common with the t. Sontag and Pyle ('43) like previous rkers, have commented on the variabil- in time of appearance of different ıters, while Greulich and Pyle ('59) like ecker ('42) listed those centers most iable, in their experience, in *order* appearance. Various workers have deoped their own ideas as to variable and ıstant centers, and have modified estites accordingly (cf. Stuart and Steven-, '54), or have weighted centers in ious ways (Acheson, '54).

The most practical way of determining relative utility of individual postnatal ification centers of the hand and wrist is discover the degree of interrelationship ıibited by each, using a complete interrelation matrix based on fully longitual data. Such an approach avoids subtivity in deciding which centers are ful and which are not, and utilizes an interrelationships to solve the priry problem.

It is the purpose of the present paper then, to present communality data on 28 postnatal ossification centers, taking boys and girls separately. In so doing, it is our hope that such data will provide the basis for a rational weighting system, as well as indicating which centers are more useful and which less useful in assessing maturity status.

METHODS AND MATERIALS

The present study is based upon serial longitudinal postero-anterior roentgenograms of the hand and wrist of 154 clinically-healthy, white single-born participants in the Fels Longitudinal Program. Subjects were selected from a total of 500 in the program on the criterion of most complete radiographic series during the first 7 years of life, and excluding like-sex siblings from the tabulations.

Since cumulative frequency curves for some of the 28 postnatal ossification centers of the hand and wrist evidenced considerable skewness, with Pearsonian coefficients of skewness up to 0.2, normalized T-scores were used (Lacey, '56; Garn and Shamir, '58, p. 82). For each sex a complete 28 by 27 correlation matrix was computed, using the N.C.R. 102-D electronic computer to minimize computational time. From the total of 1512 sexspecific correlations, communality indexes were calculated for each of the 28 bony nuclei, summing the z-transform of values of r involving that center, and then converting the mean z into the corresponding mean r (Fisher, '48). These *communality indexes*, or mean r for each center,[1] were

[1] The term "communality" as used throughout this study refers to the mean r as computed from the mean z-transforms of individual rs involving a particular center, and not to values of F^2. Complete 28 × 27 intercorrelation matrices from which the present data are derived may be obtained from the Librarian of the Fels Research Institute.

TABLE 1

Communality rankings of the ossification centers of the hand and wrist

Boys			Girls		
Center	Mean r[1]	Rank	Center	Mean r[1]	Rank
Distal IV	0.534	1	Proximal III[2]	0.613	[illegible]
Distal III	0.526	2	Proximal IV[2]	0.610	[illegible]
Distal V	0.526	3	Proximal II[2]	0.605	[illegible]
Middle IV	0.523	4	Distal III	0.591	[illegible]
Distal II	0.500	5	Metacarpal V	0.590	[illegible]
Metacarpal III	0.499	6	Middle II	0.588	[illegible]
Metacarpal IV	0.497	7	Metacarpal III	0.588	[illegible]
Distal I	0.495	8	Proximal V	0.582	[illegible]
Proximal V	0.490	9	Distal II	0.579	[illegible]
Middle III	0.490	10	Distal IV	0.574	10
Metacarpal V	0.488	11	Metacarpal II	0.571	11
Middle II	0.476	12	Middle III	0.568	12
Metacarpal II	0.472	13	Metacarpal IV	0.561	13
Middle V[2]	0.458	14	Middle IV	0.555	14
Metacarpal I	0.457	15	Distal V	0.554	15
Proximal I[2]	0.447	16	Distal I	0.552	16
Proximal II[2]	0.439	17	Middle V[2]	0.526	17
Proximal III[2]	0.436	18	Metacarpal I	0.524	18
Proximal I[2]	0.435	19	Trapezium (G.M.)[2]	0.494	19
Trapezium (G.M.)[2]	0.401	20	Trapezoid (L.M.)[2]	0.491	20
Triequetral	0.364	21	Navicular (hand)[2]	0.452	21
Trapezoid (L.M.)[2]	0.356	22	Proximal I[2]	0.413	22
Navicular (hand)[2]	0.324	23	Distal ulna	0.401	23
Distal ulna	0.301	24	Distal radius	0.361	24
Distal radius	0.277	25	Lunate[2]	0.305	25
Hamate	0.246	26	Triquetral	0.303	26
Lunate[2]	0.219	27	Hamate	0.137	27
Capitate	0.161	28	Capitate	0.123	28

[1] Mean r from mean z transforms of rs involving age at appearance of centers.

[2] Centers characterized by "irregularities in the order of appearance." (Greulich and Pyle, '5[illegible], p. 186.)

then assigned rankings in descending order of magnitude from highest (rank 1) to lowest (rank 28).

Because the radiographs from which the present data were derived, had been taken over a long time period, on subjects born between 1930 and 1951, the possibility of secular trends was explored. Inasmuch as correlations between time of birth and age at appearance of individual centers were not significant, the influence of secular trends was then ignored. Moreover, the use of pairs of centers from the same individual precluded systematic bias from this source.

It should be emphasized, however, that the correlations and the correlations involving the correlations are not independent of each other, and for that reason some of the more elaborate statistical tests were not used in the data analysis.

FINDINGS

As shown in table 1, where the mean r or "communality" index for each center is given for boys and girls separately, there is a definite heirarchy of values, differing somewhat between the sexes, but agreeing in the centers having lowest communality values. In general, girls exhibit higher communality values than boys, the order of high-ranking centers displays considerable sexual dimorphism, but the round bones of the wrist and the distal epiphyses of the forearm bones fall in the last third of the rankings (rank 20 to 28).

The sex difference in communality is highly significant by the chi-squared test, girls exceeding boys in 25 out of 28 pairings. Individual centers also tend to bear out the generalization of higher communality values for the girls, the differences being significant by t-test for 5 out of [illegible]

ıclei. However, the meaning of these fferences is weakened by the interde- endence of the correlations and therefore eans involving the correlation values. evertheless, the marked sex difference in e *order* of rankings is reflected by the ther low value of rho (0.3) between ys' and girls' communality rankings.

In attempting to rationalize the order of mmunalities, or communality rankings ıown in the table, several of the sug- stions found in the literature were sub- cted to test. The notion that communal- is a function of variability in *time* of pearance was tested, using rankings ven in table 1 and the values of sigma om Sontag and Pyle ('43) which closely atch ours. For boys, the correlation efficient r was not significant (0.27 ± 18) and it was only moderate for girls .48 ± 0.15). The alternative possibility at *relative* variability is involved was so tested, using conception-corrected lues of the coefficient of variability .V.), since assigning zero time to birth elds unrealistically high C.V. values for e early-appearing centers. Again, the rrelation was not significant for boys .21 ± 0.18) and moderate for girls .60 ± 0.12).

Greulich and Pyle ('59, p. 186) have in- cated those centers of the wrist and nd, that in their opinion are character- ed by irregularities in the order of ap- arance. As shown by footnote 2 to table the "irregular" centers do fall toward e bottom of the list in boys, but there e certain exceptions: the capitate and mate, invariably first or second in order appearance are at the bottom of the nkings, preceded by the distal radius d ulna, ordinarily 27th or 28th in order appearance. For the girls three of the ne "irregular" centers have the *highest* mmunality values, while the more or s regular hamate, capitate, distal ulna d distal radius again fall at the bottom the communality list. To some extent, the girls, variability in time of appear- ce may determine communality; to ne extent, irregularity in order of ap- arance may be related to communality ıkings.

However, it is notable that the centers ossification low in communality occupy a single anatomical area. For the boys, the last nine communality rankings encompass the carpal centers and epiphyses of the radius and ulna. In the girls, these same centers hold ranks 19 through 28, being interrupted only by the epiphysis of the proximal segment of the first digit. There is less anatomical consistency for the high-ranking centers. Even though the epiphysis of the distal segments of the digits are high-ranking in the boys (1, 2, 3, 4 and 8) and the epiphyses of the proximal segments of the digits in girls (1, 2, 3, and 8), differences between adjacent mean r or "communality" values are too small to emphasize. Only if comparable rankings appeared in an independent study would we care to assign anatomical meaning to the high-ranking centers in boys and girls respectively.

However, it is clear that, besides the sex difference in communality values, and rankings for the high-communality centers, the bony nuclei of the wrist taken as an anatomical area, have less predictive value than those of the digits or metacarpals.

DISCUSSION

It is evident, from the preceding findings, that the postnatal ossification centers of the hand and wrist differ considerably in their degree of communality. The carpal bones and anatomically-contiguous distal epiphyses of the ulna and radius exhibit rather less in common with the rest of the hand, while the epiphyses of the proximal and distal segments of the digits correlate more highly in time of ossification, with the hand and wrist in general. There is, moreover, a considerable sex difference both in the *extent* of communality, and in the particular bony nuclei exhibiting maximum communality. However, centers low in communality ranking are in excellent agreement in boys and girls alike.

Of the various explanations for the order of communalities (i.e., communality rankings) absolute variability alone seems to carry little weight. Rankings and sigma values for individual centers were not significantly correlated in boys, and only moderate in girls. Relative variability (conception-corrected to avoid implausibly-high (C.V.'s) again provided a pos-

sible explanation only for the girls. While it was true that the earliest-appearing centers (capitate and hamate) had the lowest mean *r*, the late-appearing distal ulna and radius and greater and lesser multangulars were also consistently low in communality. Therefore absolute variability, relative variability and time of appearance failed to explain the order of rankings, while purely anatomical considerations separated low-ranking and high-ranking ossification centers.

In part, centers low in communality rankings are those commonly considered to be variable in order of appearance (which is not necessarily identical with variability in *time* of appearance). The triquetral, modally 17th of the 28 centers to appear, may appear as early as 3rd or as late as 24th: it is 21st in the communality list in boys and 20th in girls. However, the distal epiphysis of the ulna, despite its consistent tendency to appear last or next to last is close to the bottom of the communality list in both boys and girls. Round bones of the wrist, and the anatomically-related epiphyses of the tubular bones of the lower arm tended to be low in communality, whether consistent in order of appearance, or high or low in relative variability.

For such practical purposes as estimating ossification status ("bone age" or percentage maturity) these communality rankings have a potential value. They suggest that presence or absence of the capitate, hamate or triquetral has little diagnostic utility, whereas the late appearance of the epiphyses of the proximal and distal segments of the digits and the metacarpals (especially the 3rd and 5th) is of greater clinical significance. Furthermore, the communality rankings given here provide a rational basis for weighting ossification centers in some system that involves percentage maturity, (cf. Acheson, '54; '57) and thus avoid purely empirical weightings (Acheson, '54, p. 503).[2]

Moreover, the sex difference in communality values and patterns emphasizes a research area of considerable interest. Boys and girls differ in the time of ossification, in the extent of communality, in the order of communality rankings, and often in the sequence of ossification of the nuclei of the hand and wrist. It is doubtful that these sex differences are mediated by steroid hormones of gonadal and adrenal origin. Anterior pituitary growth-stimulating hormone and thyroid hormone are both implicated in ossification, yet major sex differences in these hormones are by no means demonstrated in childhood. Moreover, mechanisms that affect the order of appearance of individual bony centers are quite unknown, as is the case in the order of calcification or order of eruption of the teeth. Nevertheless these early sex differences exist, and descriptive studies such as the present one serve to delineate areas for further investigative research.

SUMMARY

1. The extent of communality (average intercorrelation) of 28 postnatal ossification centers of the hand and wrist was investigated in serial longitudinal radiographs of 75 boys and 79 girls in the Fels Longitudinal Program.

2. In both sexes the carpal bones and distal epiphyses of the radius and ulna ranked low in communality (mean *r* 0.29 and 0.34), while the epiphyses of the distal digital segments ranked higher in boys (mean *r* 0.52) as did the proximal digital segments in girls (mean *r* 0.57).

3. Despite uniformly earlier ages of appearance for the ossification centers in girls, communality values for Fels girls exceeded those of boys in 25 centers with an average sex difference in mean *r* of 0.09 for all 28 centers.

4. While metacarpal and digital ossification centers appeared to be more reliable indicators of ossification status, none of the communality values could be regarded as high.

5. No satisfactory explanation could be found for the consistently higher communality values in girls, or for the sex difference in higher ranking ossification centers.

[2] Acheson's original system gave a weighting of 1 to each carpal and a weighting of but 0.2 to 0.25 to epiphyses of the phalanges and metacarpals. Later this was revised to equal weighting (Acheson, '54; '57). The present study would favor maximum weightings for the epiphyses and minimum weighting for the carpals!

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A Graphical Treatment of Temporal Changes in Some Skeletal Measurements: Graphical Osteochronology

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If a series of anatomical measurements be made on a number of similar bones of different antiquities, then, by arranging the measurements in chronological order, the morphological changes throughout the time interval between the earliest and the most recent bone can be determined. Furthermore if the measurements be plotted as Cartesian ordinates against the times as abscissae, the resulting graph will show by its gradients and curvatures exactly how the shape and size of the bone has varied with time. By extrapolating such graphs, the past history and future trends in the development of the bone could be deduced with a degree of probability dependent on the continuity of the graph and the extent of the extrapolation.

The "total morphological pattern"—to use Professor Sir Wilfred Le Gros Clark's expression—could then be deduced by comparing whole families of such graphs for as many different bones as possible.

There are many obvious difficulties in carrying out a program of this kind. They may be summarized as follows:

1. In order to obtain at least a dozen points on a graph, there must be available for measurement at least a dozen *like* bones.
2. The antiquity of each bone in years B.P. (before the present) must be known.
3. The measurements made should preferably have taxonomic significance and, if necessary, be adjusted for variations due to sex, age, etc. Only variations arising from the antiquity of the specimen will be considered in this paper.
4. Recognized anatomical measurements and indices which vary with time may either increase or decrease and are measured in different dimensional units or are non-dimensional ratios. For comparative graphical purposes it is desirable that they should all increase with time up to some fixed maximum value: for example, an arbitrary value for the average modern white adult male. Furthermore they should all be either of the same dimensions or preferably non-dimensional. How these objectives may be achieved by two simple mathematical formulas will be indicated in the following section.

Specific measurements

In order to illustrate the proposed graphical approach to the problem of hominid skeletal development or human osteochronology three particular measurements of skulls and mandibles will be considered. They are: (1) the nuchal area height index (I_1); (2) the cranial capacity (I_2); (3) the angle in the symphysial region of the mandible (I_3).

These measurements have been chosen for the following reasons: (1) Investigations mainly in Africa, Java, China, Palestine and Europe have led to the discovery of relatively large numbers of skulls and mandibles; the numbers being sufficient to enable satisfactory graphs to be produced from appropriate measurements. Other human bones have not yet been discovered in sufficient numbers for this purpose. (2) The remains have been dated with reasonable accuracy by geochronological methods. (3) They cover the whole period of man's existence upon the earth; about a million years. (4) Each measurement has recognized taxonomic value. The index I_1 gives some indication of man's erectness of posture, I_2 is related to his intellectual development and I_3 is a factor connected with his ability to have articulate speech. Each of these three criteria of humanity will now be considered in more detail.

I_1 (the nuchal area height index) is the percentage ratio of the height of the superior crest of the nuchal muscle attachment area to the auricular height of the skull: both measurements being made perpendicular to the Frankfort Plane. The index was introduced by Professor Sir Wilfred Le Gros Clark ('49) as some indication of the erectness of posture of the skeleton.

With quadrupedal gait the spine is more or less horizontal, the skull is suspended from the cranial end and hinged on the occipital condyles which, together with the foramen magnum, are situated towards the posterior part of the skull. The nuchal muscles extend relatively high up on the occipital bone in order to maintain the skull in a more or less horizontal position by counteracting the tendency of the weight of the anterior portion of the skull to tilt the face downwards.

With bipedal gait the spine is more or less vertical. The skull is not suspended from the spine but is balanced or pivoted on the cranial end and the occipital condyles and foramen magnum are more centrally situated at the base of the skull. Strong nuchal muscles are no longer needed to keep the skull horizontal with the result that they cover a much smaller area of the occipital bone, and allow the skull to expand upwards. Thus the more erect is the posture the greater will be the auricular height and the lower will be the crest of the nuchal muscle attachment area.

The ratio I_1 therefore increases with the antiquity of the skull and decreases with the more erect hominids. Being the ratio of two linear dimensions, the index is nondimensional. With modern man the crest is usually *below* the level of the Frankfort Plane with the result that the value of I_1 becomes negative. (See column 4 of table 1, and below.)

I_2 (the cranial capacity) is a dimensional measurement (usually expressed in cubic centimeters) which, in general, decreases with the antiquity of the skull in contrast to the variation with antiquity of the I_1 index. In other words modern men have larger skulls (with some exceptions) and greater intelligence than their more primitive ancestors. This measurement is ther fore of considerable significance in t evolution of the hominidae.

I_3—the angle in the symphysial regi of the body of the mandible is, like I_2, dimensional measurement (but in degre or radians). Also like I_2, it *decreases* wi increase in the antiquity of the bone. is, together with other factors, related man's ability to have articulate speec Articulate speech is less probable with constricted mouth cavity and with a tong of relatively small flexibility. With t apes the narrow and almost parallel rig and left halves of the body of the mandib and the large area of attachment of t genio-glossus muscles effectively inhibi articulate speech, especially as it is al accompanied by undeveloped inferior fro tal convolutions of the brain. With ma the splayed angle of the mandible and t flexibility of the tongue form a resona mouth cavity capable of being varied bo in size and shape. Consequently a ma with articulate speech is a possibility, b a speaking ape is an impossibility. Th the I_3 index is some measure of mar speech potentiality and therefore has co siderable taxonomic value.

With a few jaws, where the lower dent arcade is horse-shoe shaped, there is n clearly defined angle in the symphysi region. In such cases, the value of th index is indeterminate. Fortunately t measurement can be made on the majori of prehistoric mandibles.

The difficulties of plotting the values these three sets of measurements as co parable graphical ordinates will be a parent from the following figures take from table 1. The I_1 index *decreases* fro +30 with the Pithecanthropoids to – with modern man, while the cranial capa ity I_2 *increases* from 775 cm^3 to 1480 c and the mandibular angle increases fro about 25° to 48° with these two types men respectively.

It is however possible to make all the figures increase with the modernity of t bone up to (say) 100 for modern ma This can be done without altering the relative values and irrespective of the different directions of variation, differe magnitudes and different units. When t

necessary mathematical transformations have been made, the values assigned to the more primitive skeletons will measure the "percentage humanity" of the given bone at that particular time determined by the dating of the specimen.

In order to see how the measured values may be modified to meet these requirements, let I be the normal value and H the modified value of a given measurement or index, and let ${}_{P}I$ represent the value of I for the earliest and most primitive member of a series and let ${}_{M}I$ be the corresponding value for the average modern white adult male. Also let ${}_{X}I$ be the value for any intermediate skeleton. To transform values of I to the corresponding "percentage humanity" values H, it will be necessary to consider two cases: (1) when ${}_{P}I < {}_{M}I$ and when (2) ${}_{P}I > {}_{M}I$. The problem is to make ${}_{M}I = 100$ and to transform all the other indices to numbers *less* than 100 without altering their original *relative* values.

1. ${}_{P}I < {}_{M}I$. The first case is relatively simple because it entails adjusting ${}_{M}I$ to 100 and modifying the other values of I in proportion. Thus the modified value ${}_{X}H$ of any index ${}_{X}I$ is given by;

$$ {}_{X}H = 100\ {}_{X}I/{}_{M}I \qquad (1) $$

his formula is applicable to any series or which ${}_{P}I < {}_{M}I$. The second example iscussed above, namely cranial capacities $_2$, is a case in point, because ${}_{P}I_2$—the ranial capacity of *Pithecanthropus erectus I*—is less than ${}_{M}I_2$, the skull capacity of odern man.

The modified values, using equation (1) re therefore;

$$ {}_{P}H_2 = 100 \times 775/1480 = 52.2\% $$

nd

$$ {}_{M}H_2 = 100 \times 1480/1480 = 100\% $$

s required.

hus, as far as the skull capacity is conerned, the percentage humanity of *Pitheanthropus erectus II* is 52. Other values f I_2 and H_2 are given in table 1, columns and 7.

Similarly, the I_3 index increases directly ith increase in the modernity of the andible. Consequently the modified reults H_3 shown in the last column of table follow directly from the use of equation). For example:

$$ {}_{X}H_3 = 100{}_{X}I_3/{}_{M}I_3 = 100 \times 25.7/48 = 53.6\% $$

for the Heidelberg jaw or the percentage humanity of this mandible is about 54. Other values of I_3 and the corresponding values of H_3 are given in the last two columns of table 1.

2. ${}_{P}I > {}_{M}I$. In the second case, where the series of measurements increases with antiquity, the necessary modification is slightly more complicated. As before ${}_{M}H$ must equal 100. At the same time the value of ${}_{P}H$ must be less than 100 in spite of the fact that ${}_{P}I$ is greater than ${}_{M}I$. The necessary mathematical procedure can be appreciated most easily by treating the problem in two stages. First, the gradient of the graph of I against time *decreases*. This can be reversed without altering the relative values by plotting the "mirrored" or image graph as seen in a plane mirror oriented perpendicular to the axis of ordinates and passing through the origin. Suppose the image value of the ordinate corresponding to any value ${}_{X}I$ be ${}_{X}Y$, then we have:

$$ {}_{X}Y = ({}_{P}I + {}_{M}I - {}_{X}I) \qquad (2) $$

The mirrored image graph obtained by plotting the values of ${}_{X}Y$ against time will now have a positive slope. Consequently the required values of ${}_{X}H$ will be obtained directly by the use of equation (1). That is:

$$ {}_{X}H = 100\ {}_{X}Y/{}_{M}Y \qquad (3) $$

It will not be necessary to plot the (${}_{X}Y$/time) graph nor to calculate the values of ${}_{X}Y$, because it is obviously possible to eliminate ${}_{X}Y$ by combining equations (2) and (3) while at the same time substituting for ${}_{M}Y$ its mirrored value as calculated from (2). Thus:

$$ {}_{X}H = 100({}_{P}I + {}_{M}I - {}_{X}I)/{}_{P}I \qquad (4) $$

This equation gives the modified ordinate values when the value for the first or most primitive member of the original series (namely ${}_{P}I$) is greater than the value for modern man (${}_{M}I$).

When the measured values change sign it is necessary to make all the values positive before applying either equation (1) or equation (4). This is easily done by adding the largest negative value to every member of the series.

The index I_1 is a case in point. For this series ${}_{P}I_1$ was taken to be +70 for the

TABLE 1

Skulls, provernances, dates (abscissae) and skeletal values (ordinates) for the graphs of figure 1

Skull	Locality	Time (T)	Nuchal height I_1		Cranial capacity I_2		Mandibular angle I_3	
			Ratio	H_1	Vol.	H_2	Degrees	H_3
		Years B.P.		%	cm^3	%		%
Modern man	England	0	−9.0	100	1480	100	48	100
Homo sapiens	Glastonbury, Somerset	2,000	−5.7	96	1468	98	—	—
	Hutton, Somerset	5,000(?)	−7.4	97	1415	96	47	98
	Wadjak I, Java		—	—	{1650	110	28	58
	Wadjak II, Java	10,000	—	—	1550}	104	24	50
	Aveline's Hole, Somerset	17,000	—	—	1450	97	45	94
	Chancelade, Dordogne, France	30,000	—	—	1590	106	38	79
	Prědmost, Czechoslovakia	50,000	−2.9	91	{1590 1440}	{106 95}	—	—
	Cro-Magnon, France	50,000	−8.0	98	1660	111	34	71
	Coombe-Capelle, France	50,000	—	—	1580	106	—	—
Homo neanderthalensis	La Chapelle aux Saints, France	75,000	+14	70	1450 (mean)	97	26.4	55
Pithecanthropus soloensis	Solo River, Java	75,000	+25	57	1100	74	—	—
Homo rhodesiensis	Broken Hill Mine, Rhodesia, Africa	75,000	+10	76	1280	86	—	—
Homo neanderthalensis	Skhūl Cave, Palestine	150,000	{−1.6	{91	1550	104	34	71
	Tabūn Cave, Palestine	150,000	+4.6}	83}	1550	104	34	71
			+8.7	78	1270	85	27	56
	Steinheim, Germany	200,000	+17	67	1070	73	—	—
Pithecanthropus pekinensis	Choukoutien, Pekin, China	250,000	+24	58	1075	74	29	60
Homo heidelbergensis	Heidelberg, Germany	350,000	—	—	—	—	25.7	54
Pithecanthropus erectus I and II	Trinil and Sangiran, Java	400,000	{— +30}	— 51	917 775	61 52	— —	— —
Pithecanthropus modjokertensis	Modjokerto, Java	500,000	—	—	—	—	25.5	53
Australopithecus africanus	Sterkfontein, Africa	600,000	+8.9	77	{450 600}	{30 40}	38.8	81
Aborigine	Australia	0	+25	60	1200	81	25	52
Chimpanzee	Africa	0	+50	24	400	27	3.2	6.7
Proconsul africanus	Kenya, East Africa	20 to 30 million	—	—	350	24	15.2	32
		Figure 1	⟶	○		△		□

gorilla. It is +30 for *Pithecanthropus erectus* II and −9 for modern man. Hence, using equation (4), we have (for modern man):

$$xH_1 = \frac{100(79 + 0 - 0)}{79} = 100\%$$

and (for Pithecanthropus):

$$xH_1 = \frac{100(79 + 0 - 39)}{79} = 51\%$$

Other values of I_1 and H_1 are given in columns 4 and 5 of table 1.

Skeletal material and resultant graphs

In spite of the severe limitations (outlined in paragraphs 1, 2 and 3 on page 325) on the choice of suitable skeletal remains, it has been found possible to obtain sufficient values of the three selected indices to enable reasonable graphs to be drawn. In table 1 are recorded the measured values (I) together with the percentage humanity values (H) obtained from 20 prehistoric skeletons, to which have been added for comparative purposes the corresponding values for the Australian aborigine, the chimpanzee and the Miocene ape *Proconsul africanus*. The H values in table 1 are the ordinates of the graphs in figure 1.

The date allocated in column 3 of table 1 to each specimen is that which has been

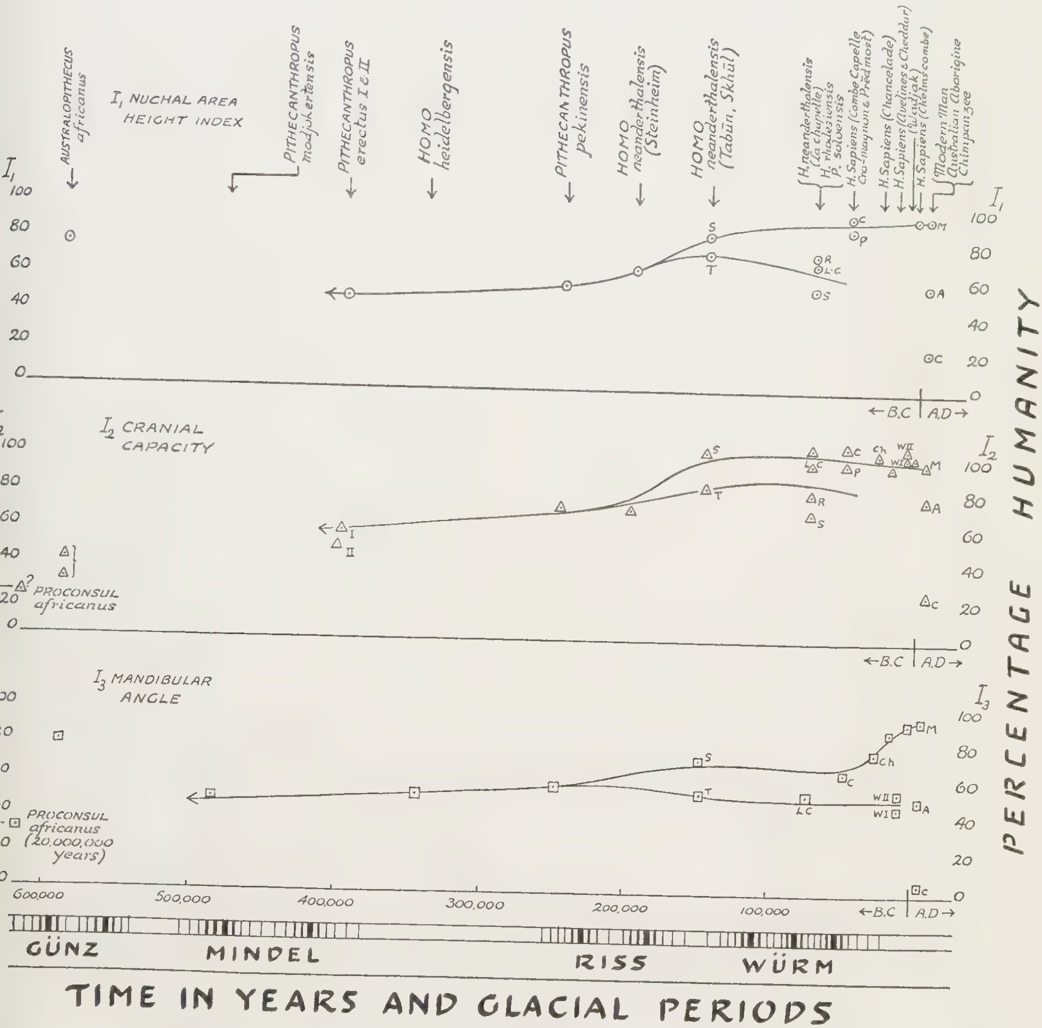

Fig. 1 Osteochronological graphs: skeletal measurements/time.

determined from the geological horizon or from dateable artifacts with which each skull or mandible was associated. The values in years B.P. (i.e., before the present) are the abscissae of the graphs. The three resulting graphs are shown in figure 1.

Some deductions from the graphs

It is not easy from a study of table 1 to see the general trend of the figures nor to realize how the data in one column compare with those from another. But when the values are plotted as in figure 1, several conclusions are at once apparent, and others can be deduced by a closer study of the graphs and their slopes or gradients. There are many large and small variations on each graph and some significant differences between them. An attempt will now be made to interpret the more important variations and to see whether any explanations are forthcoming.

1. *Linearity of the graphs.* The linearity of the graphs means that there has been a gradual temporal change in each of the three morphological characteristics under consideration. This suggests the possibility of some genetic relationship between the several types whose skeletal remains provided the osteometric data for the graphical ordinates. But the continuity of the graphs is no proof that such a relationship exists. Professor Sir Wilfred Le Gros Clark considers that, in general, it is justifiable to asume "that species and genera which show a predominance of structural resemblances are genetically related forms." ('54).

A temporal sequence of morphological characteristics is a primary criterion of a genetic relationship, and a graphical treatment of osteometric data is one of the simplest methods of determining whether or not such a sequence exists.

In the present case, any assumption of a genetic relationship is based on the continuity of the graphs of only three series of measurements which have recognized taxonomic significance. Many more measurements will therefore be necessary before an assumption of genetic connection can be accepted without reserve. But the opposite conclusion, which follows from any *dis*continuity in the plotted points, can be accepted with considerable confidence; namely, that *without* any continuity a genetic connection between the different types is highly improbable if not impossible. This follows because rapid temporal fluctuations or jumps in consecutive values of a series of osteometric measurements of genetically related types do not normally occur. This negative conclusion may be more useful than the less probable positive assumption that a continuous graph indicates some genetic relationship. (See paragraph 5 below on the Australopithecinae.)

If it now be assumed that there may be *some* genetic connection (particularly between the Pithecanthropoids) then the gradient of the graphs prior to about 250,000 B.C. not only measures the time rate of change of the particular morphological characteristic, but is also a measure of the rate of hominid evolution in as far as it can be determined from the three sets of measurements (see paragraph 2 below on the gradients).

On the whole the three graphs are unexpectedly similar especially that central part which is contemporary with the Mindel-Riss interglacial period. During this time the climatic conditions were more or less stable, producing what Jepsen, Simpson and Mayr termed a "constant genetic controlling factor." ('49). It may therefore be that the constant intensity of solar radiation was at least partly responsible for the steady rate of hominid development during this period.

It is not to be expected that the parallelism of these three graphs would apply to other indices because all the changes in man's morphology have not necessarily occurred during the 200,000 years of the Mindel-Riss interglacial, nor did they necessarily develop at the same rate. However, it is perhaps not surprising that the I_1 and I_2 graphs are more or less parallel because the reduction in the tension of the nuchal muscles with a more erect posture would allow the expansion of the skull to take place. Consequently these two changes may well be interdependent.

2. *Gradients and law of hominid evolution.* Apart from certain deviations on each graph, there is a general tendency for all the graphs to have a positive gra-

dient[1] commencing roughly at the point (400,000 years, 50%) and extending to the present time where 100% represents the degree of humanity of modern man. Consequently the percentage rate of increase per annum of the "humanity" of man as judged from the average gradient of these three graphs is $50/4 \times 10^5$ or 1.25 per 10,000 years. This is 1.25 darwins. Professor J. B. S. Haldane devised the "darwin" as a unit of evolutionary rate and defined it as the rate of change when any anatomical dimension alters in value by one thousandth part in a thousand years ('49). Thus 1.25 darwins is the rate of human evolution as determined y these three particular osteometric measurements. The time interval covered by hese graphs does not justify any considertion of the very slight curvature which esults in the gradient becoming less for nore remote times. In other words, there s a slight convexity of the graphs towards he axis of abscissae. If this curvature be eglected, these graphs show that there is rectilinear law applicable to the last 00,000 years of man's physical evolution.

This law may be stated:

$$H = 100 - \alpha T \qquad (5)$$

here H is the "percentage humanity" or rdinate value at any time T and α is the volutionary constant" for man expressed per cent per annum; that is $\alpha = 1.25 \times$ 0^{-4}. This value of 1.25 darwins for the te of hominid evolution may be comared with Dr. F. Weidenreich's value of 24 darwins. This figure is obtained from easurements of the skull length/height dex of *Pithecanthropus pekinensis* asming the antiquity of the relics to be 0,000 years. Professor J. B. S. Haldane suggested an exponential equation for calculating man's rate of physical evolution. His equation leads to a rate of 1.3 darwins using cranial capacity data.

On the whole it would appear from these graphs and from other calculations that man has evolved physically during the past half a million years at a rate of about one and one-quarter darwins.

3. *Divergent evolution of the Neanderthaloids.* An interesting variation on all these graphs is the bifurcation which seems to have taken place about 250,000 years ago. The pedomorphic or nonspecialized Neanderthaloids seem to share the general upward trend of the graphs, but the gerontomorphic or specialized Neanderthal men have developed much less rapidly. These conclusions can perhaps be appreciated most readily from the data in table 2, in which the mean value of the "percentage humanity" H determined from the three values in table 1, is compared with the value of H calculated from equation (5), using the time factor from column 3 of table 1.

The agreement between the mean values for the pedomorphic Neanderthal men is very close, but for the gerontomorphic men the mean of the measured indices is 15.5% lower than those calculated from the general law of evolution given by equation (5). This seems to suggest at least a sub-specific difference between the two types of Neanderthal men.

If the volume of the Swanscombe skull be included on the I_2 graph, the upper branch of the graph would tend to continue backwards in time more or less par-

[1] Times when plotted as abscissae are considered to increase in the direction B.C. to A.D.

TABLE 2

Measured and calculated "humanity" of the Neanderthaloids

Skull	Average H from table 1	H calculated from equation (5)	Time
Pedomorphic			*Years B.P.*
Skhūl	87	81	150,000
Steinheim	70	75	200,000
Mean	78.5	78	
Gerontomorphic			
La Chapelle	74	93	75,000
Tabūn	73	81	150,000
Mean	73.5	87	

allel to the lower branch. In this case it might be concluded that the Swanscombe man, the pedomorphic Neanderthaloids and *Homo sapiens* were genetically related and developed independently of the Pithecanthropoids and the gerontomorphic or specialized Neanderthal men. It is unfortunate that it is not possible to obtain the I_1 and I_3 measurements for the Swanscombe remains. In any case, any such theoretical conclusion, based as it is on only one measurement of one skull together with an equally approximate date for the geological horizon of the relics, means that this particular view of human evolution must be accepted with considerable reserve until more skeletal remains are discovered.

In either case, the graphs suggest the possibility that the Neanthropoids of Europe may have descended directly from the pedomorphic Neanderthaloids. If these Neanderthaloids migrated *to* the south on the advance of the last ice-age, the generally accepted idea that the Neanthropoids immigrated into Europe *from* the south would accord with the suggested genetic connection between these two types of men.

4. *Extrapolations.* Some deductions will now be made by extrapolating the graphs both forwards and backwards in time. Extrapolations are justified because of the linearity of the graphs; genetic relationships of some kind will also be assumed.

Extrapolation forwards of the upper portions of the graphs merely indicates or predicts what physical or morphological development man may anticipate in the near future. Any such extrapolation necessarily presupposes the continuation of the present conditions which control man's genetic relationships. This means that no new ice-age is anticipated and that man himself makes no appreciable artificial variations in the radiations or other genetic influences to which he is now exposed. Assuming therefore the continuation of the present conditions, none of the graphs promises any very startling changes in the next few millennia. An improvement in speech potentiality seems to be the most likely happening together with a further slight decrease in the average cranial capacity.

Extrapolation of the lower branch of the graphs pertaining to the gerontomorphic Neanderthal men leads to more interesting conclusions. Extrapolation necessarily presupposes that these Neanderthaloids did not become extinct. All the three curves pass surprisingly close to the points A (figure 1) which represent the several indices for the Australian aborigine. The Wadjak mandibles (but not the skulls) form an interesting and possibly significant link with the mandibular index of the Australian aborigine. Dr. E. K. Tratman ('50) has already noted Neanderthaloid features in Mongolian teeth. It is therefore extremely tempting to suggest that these extrapolated graphs are some evidence for the migration of the gerontomorphic Neanderthal men south and eastwards through Malay and Java to Australia during the last glacial epoch. Both Sir Arthur Keith and Dr. E. Dubois spoke of the Wadjak men as proto-Australians. *Pithecanthropus soloensis* is therefore probably another link in support of this suggested southeasternly migration of the classical Neanderthaloids. It is to be hoped that further links in the chain of evidence may be forthcoming. On the other hand Dr. G. M. Morant ('27) points out that the facial characteristics do not support such a hypothesis.

If the graphs be extrapolated backwards with due consideration for their curvature they will pass quite close to the index values for *Proconsul africanus*. This does not mean that *Homo sapiens* has descended (or ascended) from this Miocene ape, but it does mean that he could have done so. The curves so extrapolated would pass near to a percentage humanity value in the region of 30 somewhere between 20 and 30 million years ago. The indices for this ape are difficult to determine, but the H_2 index is probably about 24 (for 350 cm^3) and the mandibular angle about 15° giving a value of 32 for H_3.

5. *The Australopithecinae.* The next conclusion arises when the index values for *Australopithecus* are examined. I_1 and I_3 do not fall anywhere near their respective graphs; but the value of the skull capacity lies on the I_2 graph and accords with what would be expected from so primitive a creature living at least 500,000

years ago. The discrepancies in the I_1 and I_3 values preclude the possibility of any genetic connection with the other fossil men. In other words, the *Australopithecinae* are not ancestral to man. This conclusion accords with Sir Wilfred Le Gros Clark's view based on a study of the milk molars of these apes.

6. *The position of the chimpanzee.* The indices for the chimpanzee (Points C in figure 1) are much smaller than those for *Proconsul africanus.* This is what would be expected if the apes and men had diverged from an early man-like ape, such as *P. africanus*, at some remote time. More points are needed on graphs for both men and apes before this time of divergence can be determined graphically. In this connection it is of interest that the symphysial angle of the mandible of *Oreopithecus bambolii* from Tuscany leads to a value of about 20 for the H_3 index. Even f this be only approximately correct (for he mandible was much crushed) then his primitive ceature is ancestral to the ipes and not to man. It therefore contriputes a very distant point on the I_3 graph of the Ape family.

7. *Articulate speech.* Finally some eference must be made to the rapid inrease in the gradient of the I_3 graph about 0,000 B.P. The meaning of the change n slope is clear. The angle in the symhysial region of the mandible increased elatively rapidly towards the close of the ist ice-age. During this time the cranial apacity was slightly decreasing. Hence ny general increase in the size of the skull, uch as occurred about 200,000 B.P., could ot account for the widening of the disnce between the ascending rami of the andible. A graph of the changes in skull *idths* with time is necessary in order to arn more about possible causes for this nexpected increase in the convergence igle of the mandible.

It is probably not a coincidence that at is time man's cultural development ben to accelerate. In fact all major culral progress began about the close of the st ice-age and increased very rapidly in st-glacial times. Many authorities (for ample, White, '49) believe that speech s one of the governing factors in man's ltural development. Consequently it may be that, stimulated by the rigorous ameliorating climate of the time, man was able to acquire an ability to speak articulately and to develop his mouth cavity (and mandibular angle) at the same time. However, the points on the graph, particularly that one provided by the Chancelade mandible, leave no doubt that a significant development of man's speech potentiality took place during the years immediately following the last ice-age.

The points discussed in these 7 paragraphs do not exhaust the conclusions that can be deduced from these graphs. Particularly is this the case when they are compared with cultural development graphs, the gradients of which are practically zero for hundreds of thousands of years and then become steeper and steeper in post-glacial times (Palmer, '59). But this topic, although inseparably linked with the graphs of hominid physical development, is beyond the scope of the present discussion.

CONCLUSIONS AND SUMMARY

The foregoing graphical treatment of the temporal changes which have occurred with certain morphological features of the hominid skelton was originally outlined in a somewhat different form in "Man's Journey Through Time" (Palmer, '57). This paper discusses and supplements that portion of the book which is concerned with man's physical development. Any considerations of the evidence underlying the dating of skeletons and any discussion of the cultural aspect of man's development have been omitted. Consequently a specialized knowledge of such kindred disciplines as Geochronology and Prehistoric Archeology is unnecessary when dealing solely with the skeletal aspects of Anthropochronology, that is with Osteochronology.

After indicating a graphical method for depicting the changes that have occurred in the human skeleton in the course of time, some of the inherent difficulties of the method are outlined.

In Section II three anatomical measurements are considered, namely—(i) the nuchal area height index (ii) the cranial capacity and (iii) the angle in the symphysial region of the mandible.

These measurements are shown to have considerable taxonomic significance, and are related respectively to erectness of posture, degree of intelligence and speech potentiality.

How measurements and indices may be modified mathematically in order to yield values of "percentage humanity" suitable for use as graphical ordinates is next considered. The results are embodied in two simple equations.

Section III deals with the measurements of the selected skeletal material and their dating. Twenty-three examples are chosen which vary from modern man to the man-ape *Australopithecus*. The Australian aborigine, the chimpanzee and *Proconsul* are also included. The data recorded in table 1 lead to the three graphs of Figure 1.

Section IV is concerned with deductions from the graphs and from their extrapolations both forward and backward in time.

An approximate law of hominid evolution relating the "percentage humanity" H with the time T in years B.P. (before the present) is given by the equation:

$$H = 100 - \alpha T$$

where α is the "evolutionary constant" equal to 1.25×10^{-4} per cent per annum.

Other deductions concern the probable divergent evolution of the Neanderthaloids, a possible relationship between the classical gerontomorphic Neanderthal men with the modern Australian aborigines and the position of *Australopithecus* and the chimpanzee in relation to *Homo sapiens*.

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It is not practicable to acknowledge in detail all the many original sources upon which I have had to draw for quantitative information, but I am grateful to all those Authors, whose published measurements on skulls not accessible to me, have enabled many gaps to be filled in the data recorded in table 1.

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